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**Coexistence of three species of desert scorpions by habitat
selection**

Cao, Wei, Ph.D.

The University of Arizona, 1993

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COEXISTENCE OF THREE SPECIES OF
DESERT SCORPIONS BY
HABITAT SELECTION

by

Wei Cao

A Dissertation Submitted to the Faculty of the
DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY
In Partial Fulfillment of the Requirements
For the Degree of
DOCTOR OF PHILOSOPHY
In the Graduate College
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THE UNIVERSITY OF ARIZONA
GRADUATE COLLEGE

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SIGNED: Wei Cao 

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ABSTRACT

Coexistence is common in nature. Two fundamental conditions must meet for competitive species to coexist. First, at least one environmental dimension must be heterogeneous enough for various species to exploit it. Second, these species must show a certain degree of intrinsic potential to differentiate along this dimension. Organisms living and partitioning in mosaic habitats are often destined to coexist.

Here, I propose that habitat selection is one of the major mechanisms promoting coexistence of desert scorpions. I tested this mechanism in a three-species community (*Centruroides exilicauda*, *Vaejovis spinigerus*, and *Hadrurus arizonensis*) in the Tucson Mountain area. The results show 1) Density-independently selected habitats allowed the scorpions to survive but not to coexist. 2) The dynamic nature of density-dependent habitat selection ensured the scorpions coexistence in various situations. The reckless behavior demonstrated by the subordinate species (i.e. foraging in the face of danger from large species) confirmed this point. 3) Life-history characteristics, especially the body size of the scorpions, play a momentous role in positioning the scorpions on the arena of species interaction. Large scorpions always preempt the best habitats and become the dominant species. And small scorpions have to adjust their habitat

preferences in deference to the large.

C. exilicauda, the smallest species, is the subordinate. Its habitat use was controlled directly by the density of *V. spinigerus* and indirectly by the density of *H. arizonensis*. *V. spinigerus*, the most abundant species, tolerates many habitats. Its habitat use was molded by the density of *H. arizonensis*. Being the largest and the dominant species, the habitat use of *H. arizonensis* depended exclusively on its own density. Thus, the correlation of their selective behavior and density fostered the scorpions' coexistence in an ever changing desert environment.

CHAPTER 1. INTRODUCTION.

A. INTRODUCTION

Environmental heterogeneity provides competitors with the fundamental template of potential coexistence. For competitive coexistence to occur, the competitors must possess the intrinsic abilities to differentiate the template. These are the two very indispensable prerequisites for competitive coexistence to occur in nature.

The theory of habitat selection has developed intensively in the last four decades (see Rosenzweig 1981, 1991 for references). This theory gives a sound platform for ecologists to detect and understand the major mechanism of competitive coexistence.

Habitats differ in space and time. Such differences help to support the great diversity of each ecosystem. It has been theoretically (MacArthur and Levins 1964, 1967; MacArthur and Pianka 1966; Fretwell and Lucas 1970; Rosenzweig 1974, 1979, 1981, 1986, 1987; Lawlor and Maynard Smith 1976; Charnov 1976; Brown and Rosenzweig 1986) and experimentally (Gauss 1932; Park 1948, 1954, 1957, 1962; Holmes 1961; Connell 1961; Bovbjerg 1970; Williams 1970; Pimm, Rosenzweig and Mitchell 1985; Rosenzweig and Abramsky 1985, 1986; Rosenzweig 1986, Brown 1989; Morris 1989; Abramsky, Rosenzweig,

Pinshow, Brown, Kotler and Mitchell 1990; Abramsky, Rosenzweig and Pinshow 1991) showed that habitat selection facilitates competitive coexistence in both field and laboratory conditions. Furthermore, habitat selection may stabilize predation.

The interplay between individuals' selective behavior and population dynamics has made the theory of habitat selection applicable to the population and community level. Additionally, sophisticated machineries have been developed and successfully tested on various organisms in nature. These include the marginal value theorem (Charnov 1976), the isoleg model (Rosenzweig 1979, 1981) and isodar analysis (Morris 1988). In this dissertation, I apply such theory to the study of scorpions, one major component of a desert community.

Scorpions are predacious arthropods. Most species of scorpions are successful desert dwellers. They have an array of unique life history characteristics and share a similar environment. Most scorpion populations are extremely stable, and the paramount forces acting on them are competition and predation (Polis 1990; Polis and Yamashita 1990). It is very likely that habitat selection plays a critical role in most, if not all, of the desert scorpion communities.

The scorpion fauna in Southern Arizona is very rich in both diversity and abundance, but its ecology is poorly understood. This is especially true in the Tucson area. My aim is to understand the strength and importance of habitat selection, as a mechanism, in the organization of a desert scorpion community.

B. THE STUDY AREA AND METHODS

Three study sites, at the western side of Tucson Mountains, were selected for the field study. This area is about 15 miles from the University of Arizona, and is within the property of Sonoran Arthropod Studies, Inc. (SASI). Selection of this study area involved the following considerations. Three species of scorpions, *Centruroides exilicauda*, *Hadrurus arizonensis* and *Vaejovis spinigerus*, are quite abundant and occur sympatrically there. The habitats are reasonably heterogeneous in both flora and topography. Local weather conditions are recorded daily at SASI's weather station. The field equipment could be well monitored and protected by the people from SASI. And there is easy access.

I arranged the three sites in a south to north orientation. Site A is about 2,000 meters southwest of site B. Site C is about 500 meters northwest of site B. Site C is upstream from an old alluvial fan. And site A is downstream. Site B is in between (figure 1).

The flora is numerically dominated by triangle leaf bur-sage (*Franseria deltoidea*), saguaro (*Carnegiea gigantea*), paloverde trees (*Cercidium microphyllum* and *C. floridum*). Along the study sites, jumping cholla (*Opuntia fulgida*), prickly pear (*Opuntia phaeacantha*), white-thorn acacia (*Acacia constricta*), wolfberry (*Lycium berlandieri*) and ocotillo (*Fouquieria splendens*) also occurred, but less abundantly. Creosote bush (*Larrea tridentata*) was rare in the area. More annual

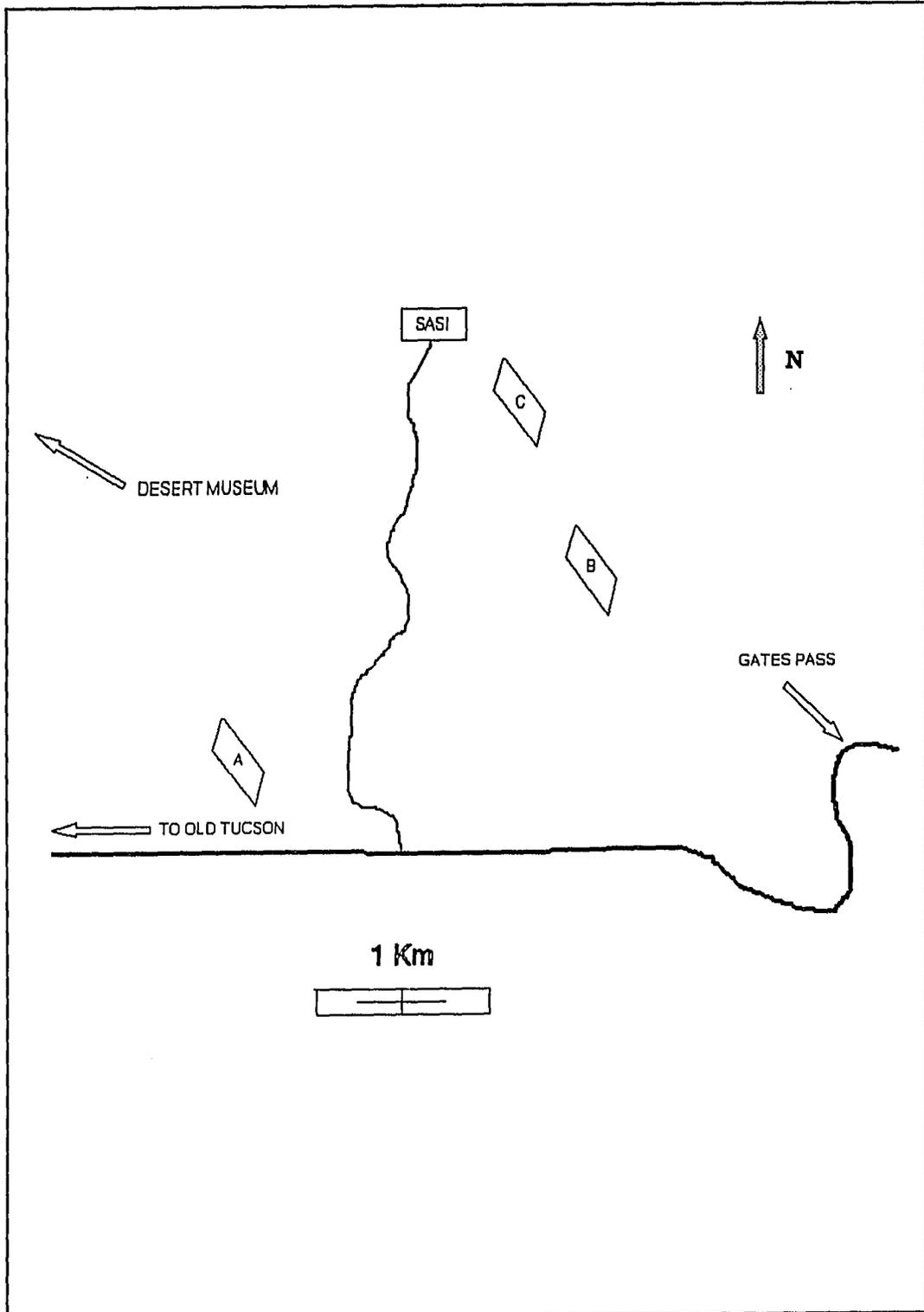


Figure 1. Schematic map of the study area.

plants occur in site A than in site C. The vegetation density increases from site C to site A. This trend follows the gradients of increasing soil fineness, moisture and temperature. All these changes correspond to elevation.

There are more larger soil particles (>2 mm) in site C than in site A. There are more small particle (<0.016 mm) components in the soil of site A than in site C. The soil texture of site B is intermediate between site A and site C.

The topographies are different for the three study sites. Site A is located on the east side of a major wash, with a 20 to 30 degree slope facing west. Site C is on the opposite hill of the west side of another major wash. It has a 10 to 20 degree slope, which is also facing west. Site B is located on a flat area.

I used forty-five cylindrical cans, commercial standard #3, as pitfall traps in the study area. Each can was buried so that its open end was flush with the ground surface. Every can was covered by a purposely-sized and marked rock. Red ribbon was tied to a nearby plant to flag each can spot. None of the cans were baited. Before burying them, I cut three unconnected slits at the closed bottom end of each can for water drainage. I numbered each can with red fluorescent paint (Liquitex, No. 1002-983) on the side wall for identification.

Fifteen cans were buried in each of the study site. They are arranged in the following way: Five cans in a row and three in a column formed a parallelogram, with every pair of adjacent cans separated by about 10 meters. (figure 2). The longer axis of the parallelogram forms an approximately

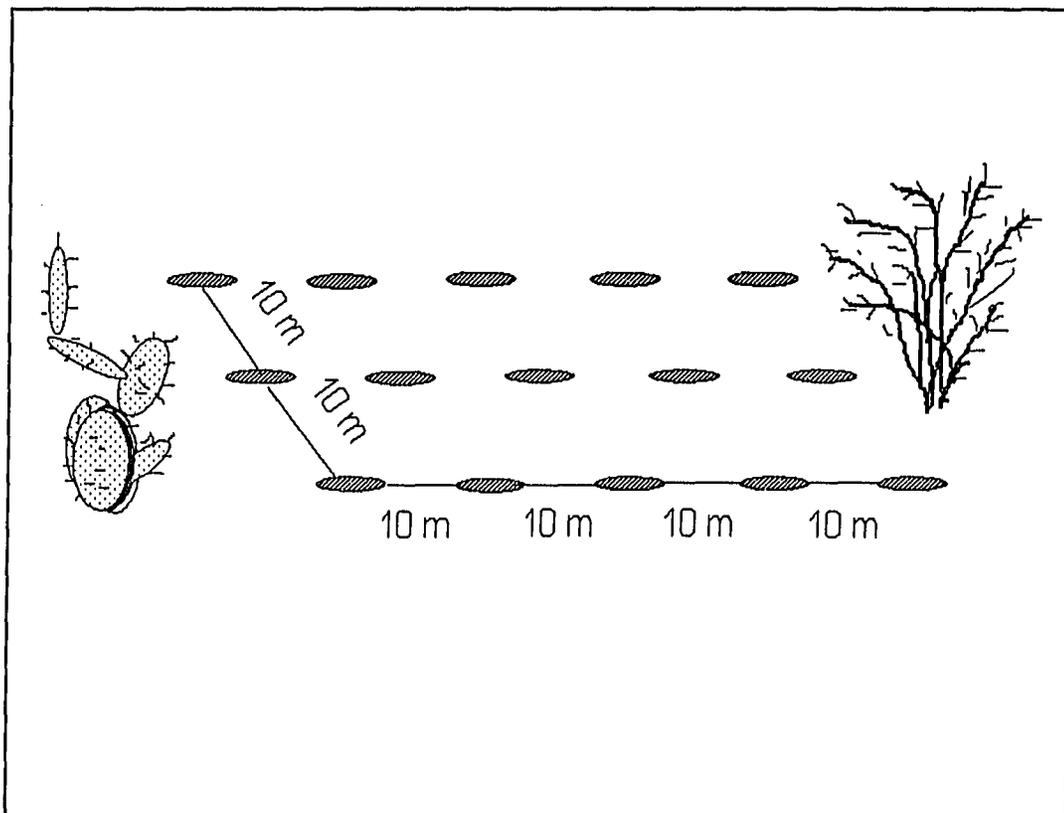


Figure 2. Schematic of experimental design of one study site. Each ellipse represents a trapping can buried on the ground. Every pair of adjacent cans were spaced ten meters apart. The boldfaced numbers are the can identifications.

forty-five-degree angle with the main flowing direction of the alluvial fan.

In the study sites and adjacent area, I also used an ultraviolet light purchased from Optronics (BlackEye, UK DES No. 994511). This light helped me to estimate the scorpion populations and to observe scorpion activities at night.

In 1991, nine discrete nights and forty seven-early-mornings were spent in the study sites. Except for one night and two morning trips, all the rest were always rewarding in terms of observing and trapping scorpions. I checked the pitfalls in early morning, from 04:30 hr to 09:00 hr Mountain Standard time. Scorpions encountered during the night trips were recorded by species, locality, time and the behavior I first observed them do. However, they were not handled or marked.

The trapping cans were checked once every two days during May 1991; twice a week from June to the 11th of October; and once per week thereafter. The census period ended in October 27, 1991. To prevent the unnecessary killing of scorpions by the trapping cans, I filled all the cans with small rocks and left them uncovered after the last day of the census period. Most of the cans were reused in the experiments of 1992.

A trapped scorpion was picked out from the can with a pair of bamboo chopsticks and marked individually by red fluorescent paint (Liquitex, No. 1002-983). The animals' sex, pedipalp length and development stage were recorded.

Marked scorpions were released about 1, 3, or 5 meters away from the spot they were trapped, according to the exact position of the cans within the parallelogram. If they were captured in the peripheral cans, on the edge of the parallelogram, they were released about 5 meters toward the center of the study site. If they were captured in other cans except the central one, then they were released three meters toward the center of the parallelogram (see figure 2). And if the scorpions were captured in the central can, then they were released about 1 meter away from the can in a random direction. The purpose of doing this is to try to increase the probability of recapturing in the future.

The coding system, which I used to mark the scorpions, based on 1) dotting a tail segment (metasoma); 2) the number of dots on the back (dorsal mesosoma); and 3) the arrangement of dots on the back. Five segments of the tail plus the telson allow for a base six number system. The number and arrangement of dots on mesosoma indicate the place in the base six system. Number 5 individual, for instance, carries only one dot - at the segment next to its telson. Number 12 individual carries two dots - one on its back and another at the tail segment next to telson, just like the one carried by scorpion number 5. The maximum number of dots I marked on the back of a scorpion was three. The number of ways to arrange three dots is far beyond the number of scorpions I could mark.

The fluorescent paint, used in both marking scorpions and coding trapping cans and cover rocks, has been experimentally proved safe for the animals. It is

also long-lasting. Some marked scorpions in captivity have carried the same mark more than two years. No significant side effect on behavior or mortality has been observed for those marked scorpions either in the study area or in laboratory captivities.

Throughout the course of study, trapping cans are maintained in the field as needed. This includes replacing rusted ones; taking out gravel, sand and trapped animals from the cans; and keeping the cans flush with the ground level.

CHAPTER 2. LIFE HISTORY, DEMOGRAPHY AND BEHAVIOR.

A. INTRODUCTION

The order Scorpiones is a small group of terrestrial arthropods with many unique life history characteristics. Unlike most other arthropods, a large number of species of scorpions belong to the category of K-selected organisms (MacArthur and Wilson 1967, Pianka 1970). Compared with other species of arthropods, they have a relatively high longevity, a slow development period, reasonably large body size, and produce a small number of offsprings. Their survivorship is high and density dependent. Because of their long evolutionary history, they are closely adapted to the environments in which they are living. Ecological niches have been well allocated and population sizes are stable. Population interactions are the prominent impact structuring scorpion communities.

B. LIFE HISTORY OF THE SCORPIONS

Knowledge of scorpion life history is crucial to understanding the system of coexisting scorpion species. But my main experimental concern focused on the habitat use and the associated behaviors of the scorpions. Thus, the information about the life history characteristics of the scorpions comes mostly from the

literature. The major life history characteristics discussed in this section are summarized in table 1.

1). *Centruroides exilicauda*

The Buthidae family separated from the phylogenetic line of the remaining scorpion families as early as the Silurian, about 435 million years ago. Some unique life history characteristics occur in most members of this family. They are commonly called the "bark scorpions" due to their arboreal life style. All the extant scorpions lethal to humans are Buthids.

Adult *C. exilicauda*, in general, range from 5.0 to 6.5 cm in body size (from chelicera to telson). But this measure varies considerably among populations. Williams and Hadley (1967), for instance, found that *C. exilicauda* in Cholla Bay, Mexico could reach 7.0 cm. The average body size of *C. exilicauda* in my study area is 5.58 cm. Males are usually smaller than females. Their bodies and appendages are more slender than those of the other species. Body coloration ranges from light yellow to dark brown, depending on the habitat. Normal individuals can live 5 years (Stahnke 1966, Williams 1969).

C. exilicauda is iteroparous. Inseminated females can produce two broods per year, and continue to reproduce without mating (Kovoor et al. 1987). Reproduction takes place from May to October. A female can have 7 to 42 offspring per litter with an average of 20 (Stahnke 1966; Williams 1969). The new

Table 1. General life history characteristics of the scorpions.

species	<i>C. exilicauda</i>	<i>H. arizonensis</i>	<i>V. spinigerus</i>
1. reproduction mode	iteroparity, reproduce two broods per year.	iteroparity, reproduce one brood pre year.	iteroparity, reproduce one brood per year.
2. reproduction time	May to October.	August.	late June to early July.
3. average litter size	20	10	35
4. number of instars	6 to 7	7	5 to 7
5. average months required for maturity	18	60	24
6. average adult body size (chelicera to telson; mean±se cm)	5.58±0.09 (n=59)	9.99±0.30 (n=58)	6.88±0.10 (n=212)
7. longevity (year)	5	25	?

born spend 6 to 15 days (the first instar stage) on the dorsal part of their mother before dispersing. Usually, six to seven instars have to be passed in order to reach sexual maturity (Stahnke 1966; Williams 1969). Males mature faster than females. It takes about 18 months for a newborn to reach maturity (Stahnke 1966; Williams 1969; Polis 1990).

2). *Hadrurus arizonensis*

H. arizonensis, in the family Iuridae, is the largest scorpion in the New World. Adults of this species can reach a body size from 10.2 to 10.8 cm. Males are little bit bigger than females (Gertsch and Allred 1965). In the population I studied, the average body size is 9.99 cm; and females are bigger than males. Visible golden brown hairs grow on the pedipalps, the legs, and the metasoma. Thus, they are commonly called the "giant hairy scorpions."

H. arizonensis is one of the K-selected scorpion species. They can live for 25 years; and reproduction takes place only after the individuals become five years old (Stahnke 1966). Similar to *C. exilicauda*, *H. arizonensis* is also iteroparous, but inseminated females only reproduce once per year. On average, a female gives birth to 10 offspring per litter (Williams 1969). The time of reproduction is synchronized in August (Williams 1969). During my two year study, only one juvenile of this species was trapped.

3). *Vaejovis spinigerus*

V. spinigerus belongs to the largest family of Scorpiones, Vaejovidae. Despite its numerical dominance in some areas, this species has been little studied. The average body size of adults, in my study area, is 6.88 cm. Females are a bit larger than males. Dark, longitudinal stripes on the rigid segments of metasoma give this species its common name "the striped tail scorpion."

In contrast to *H. arizonensis*, this species has life history characteristics that make it an imperfect member of the K-selected group. Like *C. exilicauda*, *V. spinigerus* is also an iteroparous species, but unlike *C. exilicauda*, inseminated females only give birth once per year (Williams 1969; Polis 1990). For the *V. spinigerus* population in my study area, reproduction started during the middle of June and lasted about 15 days. Newborn spent 7 to 8 days on the back of their mother (McAlister 1960; Stahnke 1966). This completes the first instar. To mature, a newborn must pass five to seven stages of instar (Polis 1990). The reported litter size, on average, was 35.5 (Stahnke 1966, Williams 1969). But I have seen one female *V. spinigerus*, in my study area, carry 27 newborn on her back. The litter size, as do other life history characteristics, probably varies in time and space.

Longevity for this species remains unknown.

C. DEMOGRAPHY

For clarity, I summarize the demography data in table 2. The results are based on the data I collected in 1991 and 1992, except where indicated otherwise.

1). Abundance

The scorpion community, in the western part of the Tucson mountains is numerically dominated by *V. spinigerus*. About 74% of the 639 total trapped scorpions during my two year study period were *V. spinigerus*. *C. exilicauda* and *H. arizonensis* made up only 14.39% and 11.58% of the community respectively (table 3). About 31% of the trapped *V. spinigerus* were juveniles in their second or third instar. However, youngsters of *C. exilicauda* were never trapped in the pitfalls. This could reflect the fact that early age instars of *C. exilicauda* might spend their entire development stages on vegetation and feed on small insects associated with plants. Similarly, only one youngster of *H. arizonensis* was trapped during my study time. This, I think, is because of: 1) the reproductive rate of *H. arizonensis* is low; 2) *H. arizonensis* is a new immigrant to this area (Prchal, pers. comm., 1991) and the effective population for reproduction is low. *H. arizonensis* started to inhabit this area about a decade ago.

Table 2. Demography of the scorpions.

species	<i>C. exilicauda</i>	<i>H. arizonensis</i>	<i>V. spinigerus</i>
1. abundance	14.39%	11.58%	74.00%
2. sex ratio (female/male)	17/75	29/45	132/196
3. population density (indiv. per 100 ² meters)	4.3	5.7	12.9
4. birth rate	?	?	31.3%
5. death rate	11.1%	?	9.6%

Table 3. Total capture of scorpions in 1991 and 1992.

species		<i>C. exilicauda</i>	<i>H. arizonensis</i>	<i>V. spinigerus</i>
study site				
year				
1991	A	14	16	92
	B	17	9	75
	C	14	6	82
	TOTAL	45	31	249
	PERCENTAGE	13.85%	9.54%	76.62%
1992	A	20	24	69
	B	9	10	63
	C	18	9	92
	TOTAL	47	43	224
	PERCENTAGE	14.97%	13.69%	71.34%
GRAND TOTAL		92	74	473
PERCENTAGE		14.39%	11.58%	74.00%

Table 3. Total captures of scorpions in 1991 and 1992. The data are from the pitfall trap captures only, include recaptures and trapped dead and young *V. spinigerus*.

2). Sex ratio

Sex ratio of the trapped adult scorpions during my two-year study is summarized in table 4. Due to the limits of pit-fall trapping, the sex ratio is biased toward males.

Among the recaptured individuals of *C. exilicauda* during my study period, there was only one female, and the rest were exclusively males. This may result from the mating process of *C. exilicauda*. Courtship of this species was initiated by males approaching females (Polis 1990). Therefore, males have to travel around to find females. This travelling significantly ($X^2=36.57$, d.f.=1, $p<<0.001$) increases the probability of males being trapped in the pitfall traps.

The sex ratio of *H. arizonensis* is also biased to males, but statistically insignificant ($X^2=3.46$, d.f.=1, $p>0.05$). Because individuals of this species only move around on the ground during the mating season, the insignificant sex ratio might indicate that courtship of *H. arizonensis* could be initiated by either males or females.

Due to their vagrant lifestyle, the significant difference ($X^2=12.49$, d.f.=1, $p<0.001$) in sex of the trapped *V. spinigerus* is only suggestive that courtship is probably initiated by males most of the time. Nevertheless, males did travel more often than females do. This is obvious by looking at the trapping data of 1992. During that year, more female individuals were marked in the field, but again, as in 1991, more males were retrapped in the pitfall traps.

Table 4. Sex ratio of the scorpions in 1991 and 1992.

year	species sex	<i>C. exilicauda</i>		<i>H. arizonensis</i>		<i>V. spinigerus</i>	
		female	male	female	male	female	male
1991	marked individuals	6	24	9	15	33	69
	total captured	6	39	12	19	53	116
1992	marked individuals	10	19	14	20	60	50
	total captured	11	36	17	26	79	80
1991+	marked individuals	16	43	23	35	93	119
1992	total captured	17	75	29	45	132	196

Table 4. Sex ratio of the scorpions in 1991 and 1992. The data are from the pitfall trap captures only. The 'marked individ' includes the scorpions that were released alive after the first time they were trapped and marked in the field. The 'total captured' are those that, in addition to the 'marked individ', includes the recaptured and scorpions that were dead when trapped first time in the pitfall traps. Only adult scorpions' sex are recorded during the entire study period due to the fact that gender is difficult to identify for young age groups.

3). Population density, birth rate and death rate

In my study area, the estimated population densities, measured as individuals per 100 square meters, were 4.3 for *C. exilicauda*; 5.7 for *H. arizonensis*; and 12.9 for *V. spinigerus*. The calculations were based on the data collected during 1991.

Birth rate was 31% for *V. spinigerus*. My data were not sufficient to calculate the birth rates for both *C. exilicauda* and *H. arizonensis*.

Death rate was 11.1% for *C. exilicauda*; 9.6% for *V. spinigerus*. The death rate for *H. arizonensis* was hard to estimate, because I never saw even one dead *H. arizonensis* in the pitfalls. Drowning during heavy rain and getting eaten by *H. arizonensis* are the main causes of mortality for adult *C. exilicauda* and *V. spinigerus* in my study area.

D. BEHAVIOR

Scorpions, in general, are mysterious creatures. They do not spend much time on the ground surface. And they spend a great proportion of their time doing one thing - hiding (Williams 1987; Polis 1990). The scorpions in my study area are no exception. To interpret my data from the scorpions' behavioral point of view, I have to assume: 1) the scorpions are randomly distributed in each of my study sites; 2) the number of trapped scorpions proportionally represents their

true activity density on the ground surface. From now on, I use the phrase "ground activity" to refer to any scorpion activity on the ground surface; and the phrase "ground period" to refer to the number of consecutive nights in which a scorpion will show some ground activities. I use the phrase "underground activity" to refer to all activities of a scorpion that do not belong to the ground activity; and I use the phrase "underground period" to refer to the number of consecutive nights in which a scorpion will not show any ground activity.

For clarity, I have summarized scorpion behavior in table 5.

1). Seasonality

a. Annual ground activity

Seasonal ground activities of the scorpions, in my study area, vary from species to species (figure 3). Adults of *C. exilicauda* are active on the ground all year round. However, the ground activity becomes more frequent from May to September. In 1991, the ground activity of *C. exilicauda* was considerably more stable from month to month during the sampling period. In contrast, individuals of *H. arizonensis* appeared on the ground surface for a relatively short time period - from the mid of June to the end of October. The highest ground activity occurred in the middle of July. Yet, adult *V. spinigerus* were active on the ground from early April to the end of October. And their ground activity became highest in early September. Juveniles of *V. spinigerus*, born in late June, were becoming

Table 5. Some behaviors of the scorpions.

species	<i>C. exilicauda</i>	<i>H. arizonensis</i>	<i>V. spinigerus</i>
1. active months	all months.	mid Jun. to end of Oct.	early Apr to end of Oct.
2. under ground period (days) (mean±se)	15±2.87 (n=15)	27±6.50 (n=7)	19±2.20 (n=67)
3. temperature effect on ground activity	no X ² =4.760 d.f.=3;p>0.10	yes X ² =14.834 d.f.=3;p<0.01	yes X ² =13.470 d.f.=4;p<0.02
4. precipitation effect on ground activity	no X ² =3.208 d.f.=3;p>0.30	yes X ² =13.094 d.f.=3;p<0.01	yes X ² =27.763 d.f.=4;p<0.001
5. luminous intensity effect on ground activity	yes X ² =15.600 d.f.=2;p<0.001	no X ² =5.870 d.f.=2;p>0.05	yes X ² =94.289 d.f.=2;p<0.001
6. active hours on the ground	all night	20:00-04:00	20:00-04:00
7. peak hours of ground activity	no	21:00-23:00	21:00-24:00
8. aggregation behavior	present in winter.	absent.	present during rains.
9. water drinking behavior	present.	absent.	absent.
10. burrowing behavior	absent.	present.	capable, but rarely do so.
11. ground foraging tactics	moving-around.	sit-and-wait.	moving-around & sit-and-wait.
12. traveling distance (mean±se meters)	10.65±2.75 (n=15)	10.97±7.12 (n=7)	19.28±2.36 (n=67)
13. prey-dragging behavior	yes	no	sometimes
14. micro-habitat use	tree, shrub, cacti, rocks.	fine-substrate ground.	rocky ground,

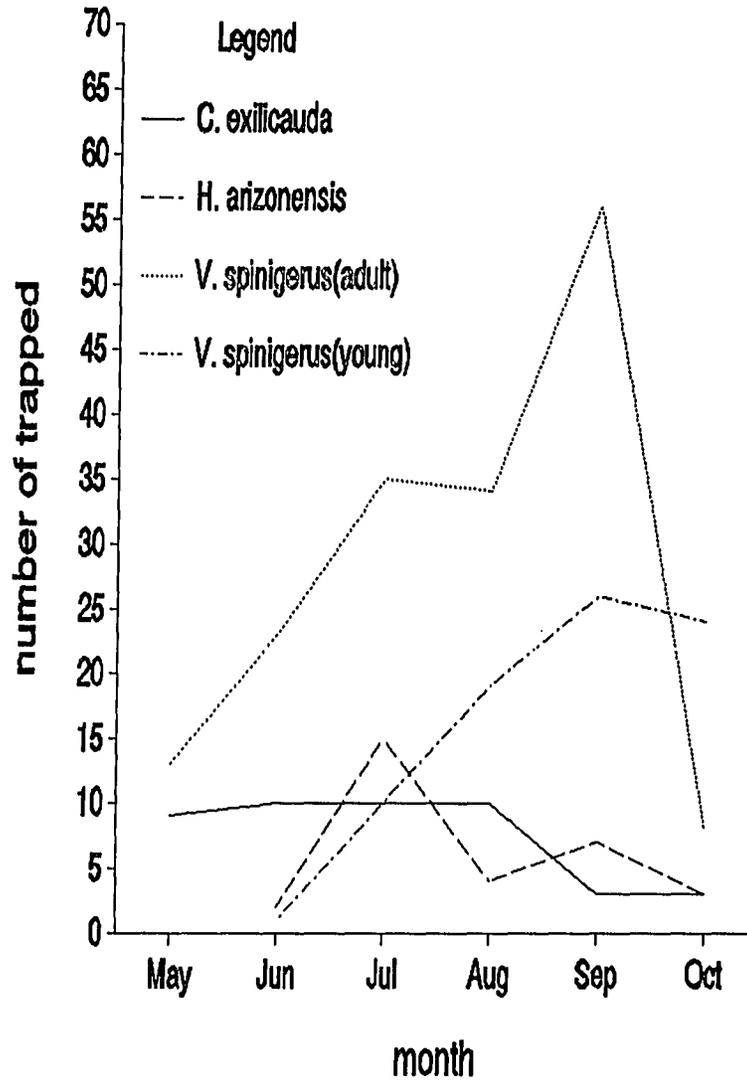


Figure 3. Seasonal ground activities of the scorpions as represented by the number of individuals trapped in each month.

more and more active on the ground until the middle of September.

The ground activities of both *H. arizonensis* and adult *V. spinigerus* declined in August - the hottest month. In contrast, the ground activities of *C. exilicauda* and young *V. spinigerus* did not change during this month.

b. Ground activity cycle

Scorpions are well adapted for intermittent feeding and infrequent activity (Toren, 1973; Polis, 1980; Williams, 1987; Benton, 1992). A large proportion of the sporadic pattern of ground activity might be explained by the scorpions' successful foraging and low metabolic rate. I have measured none of these parameters in my study. However, from the body size measurement and time intervals of the recaptured scorpions, the general relationship between body size and underground period of the scorpions emerges (figure 4). The larger the scorpion the more time it spends underground.

Calculated from 15 recaptures of *C. exilicauda* in 1991, the number of days between consecutive captures was 15 ± 2.87 (mean \pm se) with a range of [2, 39] days; from 7 recaptured *H. arizonensis*, the number of days between consecutive captures was 27 ± 6.50 (mean \pm se) with a range of [7, 53] days; and from 67 recaptures of *V. spinigerus*, the number of days between consecutive captures was 19 ± 2.20 (mean \pm se) with a range of [2, 77] days. The average body size of each species is calculated from all the adults trapped in 1991. The results (average \pm standard error) are 5.58 ± 0.09 , 6.88 ± 0.10 , and 9.99 ± 0.30 centimeters for *C.*

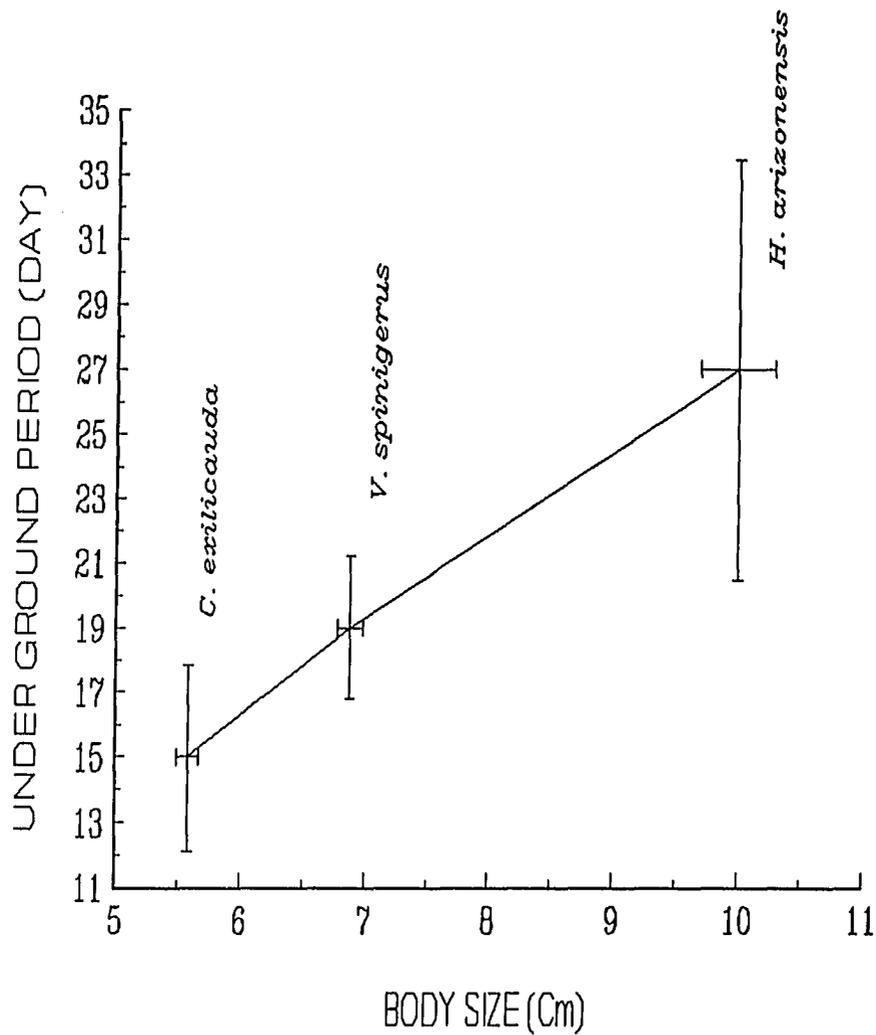


Figure 4. The association of body size and under ground period of the scorpions. The body sizes of each species are measured from chelicera to telson. For *C. exilicauda* the average body size (ABS) = 5.58 ± 0.09 Cm and the average surfacing day (ASD) = 15 ± 2.87 Cm; for *V. spinigerus* ABS = 6.88 ± 0.10 and ASD = 19 ± 6.50 ; for *H. arizonensis* ABS = 9.99 ± 0.30 Cm and ASD = 27 ± 6.50 . The linear regression line is in the form of $Y = 0.174 + 2.695X$, with $R^2 = 0.998$.

exilicauda, *V. spinigerus*, and *H. arizonensis* respectively.

Assuming that body size is positively correlated with foraging success and negatively correlated with metabolic rate, then body size could be the reliable index to predict the underground period of the scorpions.

c. Ground activity and temperature

Weather conditions, such as temperature, precipitation and luminous intensity, also influence the activities of the scorpions. Using the data of the total trapped adults scorpions from 1991, and the data from "Local Climatological Data," documented by National Oceanic And Atmospheric Administration (NOAA), I have grouped the trapped individuals of each species into five ranges. The ranges were classified on the basis of the average temperature of the trapping week (see table 6). Because the temperature records I used in this analysis were the daily averages, and because I use these daily averages to calculate the weekly averages, I have eliminated extreme temperature records. I call the temperature, treated in this way, the weekly-mean-of-daily-averaged temperature.

To test the hypothesis that the ground activity of the scorpions depends on temperature, I did a series of X^2 -tests. The ground activities of both *H. arizonensis* and *V. spinigerus*, the two ground species, are significantly correlated with the weekly-mean-of-daily-averaged temperatures. For *H. arizonensis* $X^2=14.834$, d.f.=3, $p<0.01$ (figure 5); and for *V. spinigerus* $X^2=13.470$, d.f.=4,

Table 6. Trapping frequency of the scorpions in different temperature ranges.

temperature (°F)	66-70	71-75	76-80	81-85	86-90
frequency (week)	2	3	5	8	8
species	scorpions being trapped				
<i>C. exilicauda</i>	2	5	9	9	20
<i>H. arizonensis</i>	1	0	4	7	19
<i>V. spinigerus</i>	4	15	28	53	69

Table 6. Trapping frequency of the scorpions in different temperature range. Data come from the total trapped adult scorpions in 1991. Temperature data are based on the daily average of "Local Climatological Data" documented by National Oceanic and Atmospheric Administration (NOAA). The temperature range are categorized by taking weekly average over the daily averages.

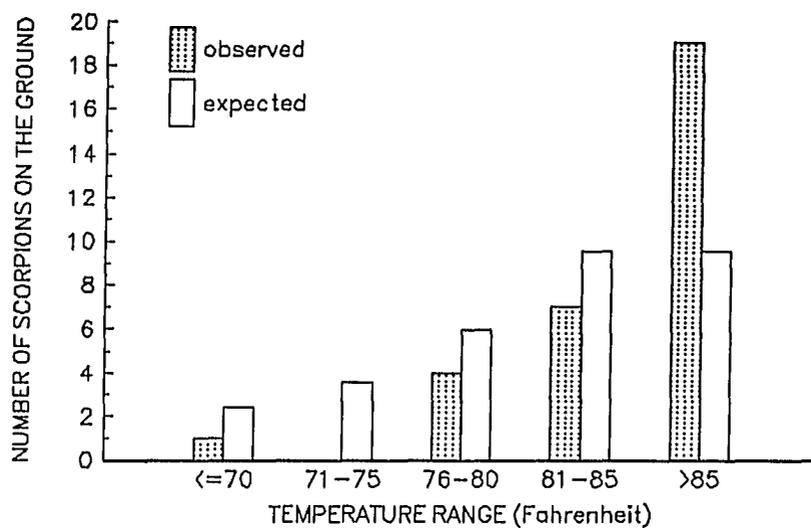


Figure 5. The association of *H. arizonensis*' ground surface density and temperature range. The expected bars were generated from a random distribution according to the number of weeks located within each of the temperature ranges. $X^2=14.834$, d.f.=3, and $p<0.01$.

$p < 0.02$ (figure 6). In contrast, the ground activity of the arboreal species, *C. exilicauda*, is not significantly correlated with the weekly-mean-of-daily-averaged temperatures, $X^2 = 4.760$, d.f.=3, $p > 0.10$ (figure 7). Correlations of activity and temperature have been demonstrated by other authors with other species of scorpions (Shorthouse, 1971; Bacon, 1972; Polis, 1980a; Benton 1992).

d. Ground activity and precipitation

Using the same data set as above, but grouping each species of scorpions into five categories based on the total rainfall received in each trapping week, the ground activities of the scorpions corresponding to precipitation can be analyzed (see table 7).

Again, the ground activities of the two ground species were positively correlated to the weekly total of rainfall. But the ground activity of the arboreal species was not significantly affected by the weekly total of rainfall. A series of X^2 -tests conducted to test the hypothesis that the surface activity of each species is independent to the amount precipitation received on the ground have confirmed the results. For *H. arizonensis* $X^2 = 13.094$, d.f.=3, $p < 0.01$ (figure 8); for *V. spinigerus* $X^2 = 27.763$, d.f.=4, $p < 0.001$ (figure 9); and for *C. exilicauda* $X^2 = 3.208$, d.f.=3, $p > 0.30$ (figure 10). During heavy rains, ground activities of the scorpions were significantly reduced. Immediately after the rains, ground activities increased dramatically for the ground species. But such change was unnoticeable for the arboreal species.

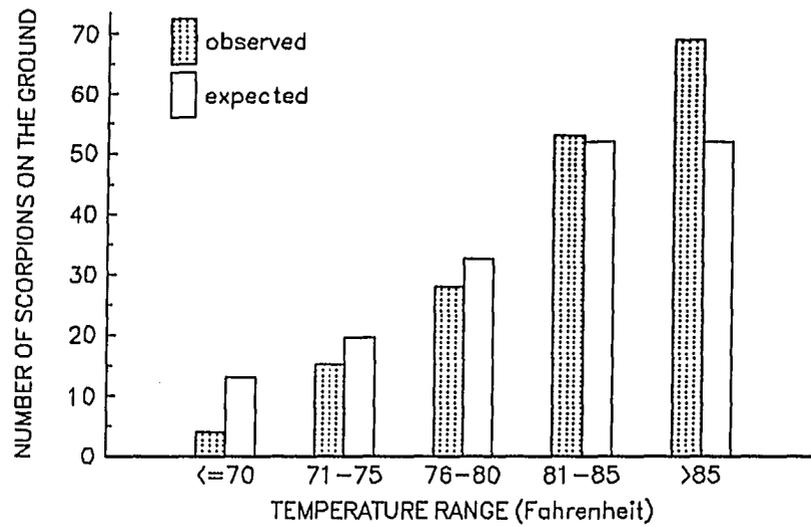


Figure 6. The association of *V. spinigerus*' ground surface density and temperature range. The expected bars were generated from a random distribution according to the number of weeks located within each of the temperature ranges. $X^2=13.470$, d.f.=4, and $p<0.02$.

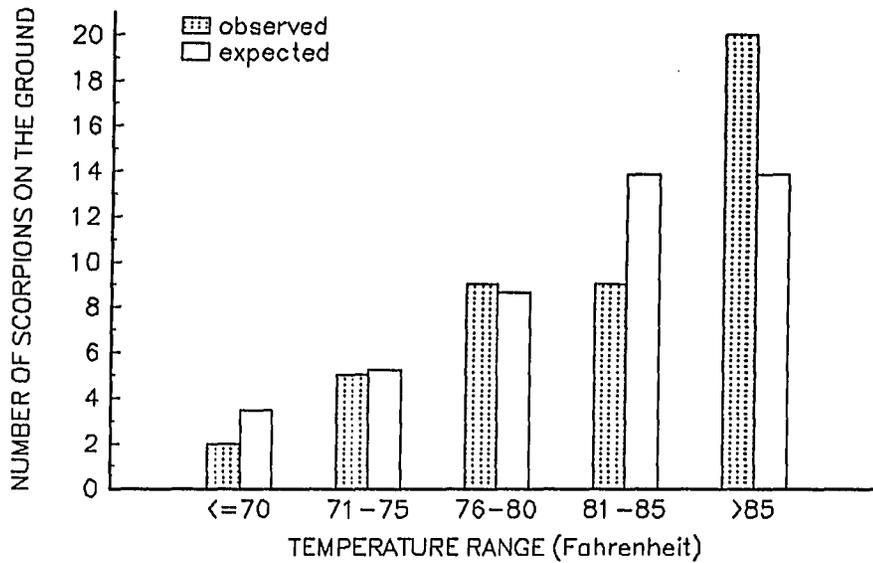


Figure 7. The association of *C. exilicauda*'s ground surface density and temperature range. The expected bars were generated from a random distribution according to the number of weeks located within each of the temperature ranges. $X^2=4.760$, d.f.=3, and $p>0.10$.

Table 7. Trapping frequency of the scorpions in different precipitation range.

rainfall (inches)	0	X·10 ⁻³	X·10 ⁻²	≥1·10 ⁻¹	≥2·10 ⁻¹
frequency (week)	9	8	4	3	2
	scorpions being trapped				
species					
<i>C. exilicauda</i>	17	9	10	2	7
<i>H. arizonensis</i>	3	17	7	1	3
<i>V. spinigerus</i>	27	69	34	20	19

Table 7. Trapping frequency of the scorpions in different precipitation range. Data come from the total trapped adult scorpions in 1991. Precipitation data are based on the daily average of "Local Climatological Data" documented by National Oceanic and Atmospheric Administration (NOAA). The rainfall categories are calculated according to the weekly sum of the daily precipitation records. The 'X' represents any single digit from 1 to 9.

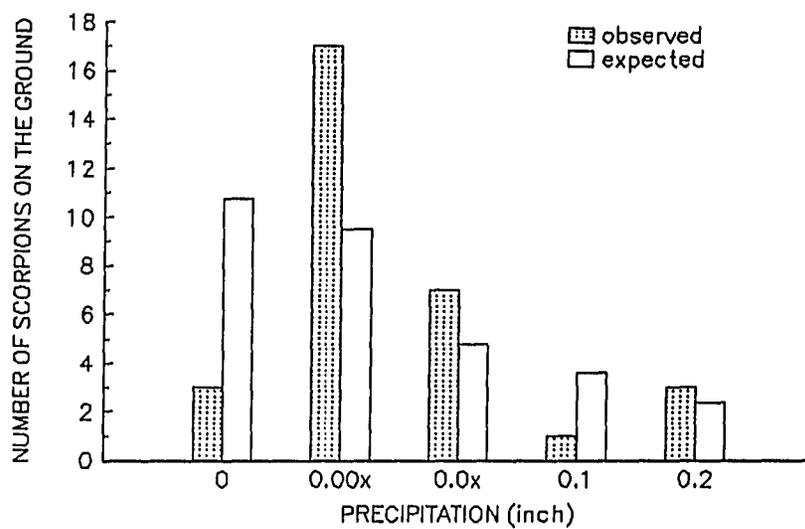


Figure 8. The association of *H. arizonensis*' ground surface density and precipitation range. The expected bars were generated from a random distribution according to the number of weeks located within each of the precipitation ranges. $X^2=13.094$, d.f.=3, and $p<0.01$.

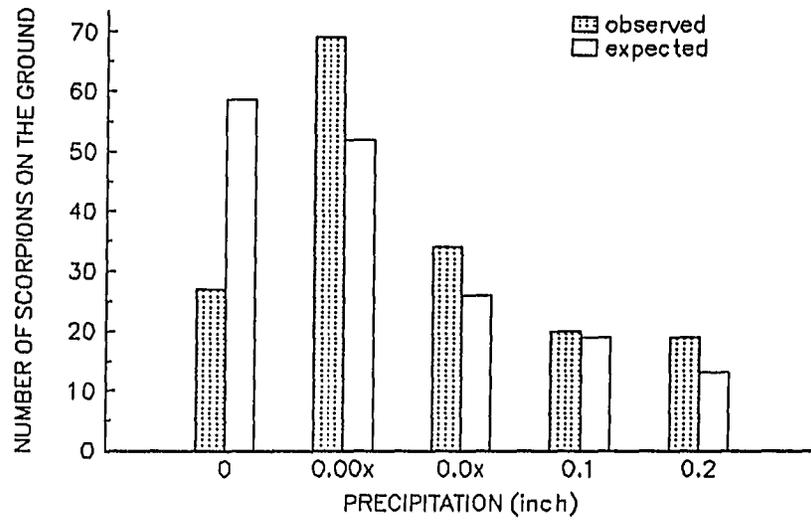


Figure 9. The association of *V. spinigerus*' ground surface density and precipitation range. The expected bars were generated from a random distribution according to the number of weeks located within each of the precipitation ranges. $X^2=27.763$, d.f.=4, and $p<0.001$.

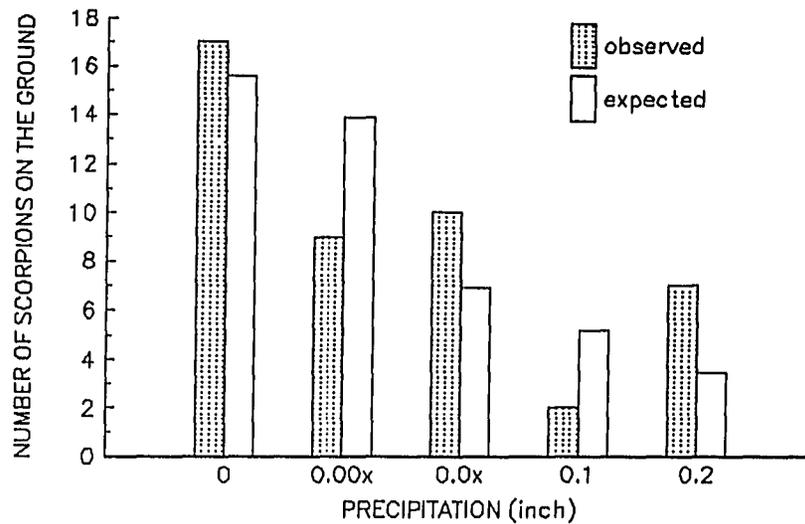


Figure 10. The association of *C. exilicauda*'s ground surface density and precipitation range. The expected bars were generated from a random distribution according to the number of weeks located within each of the precipitation ranges. $X^2=3.208$, d.f.=3, and $p>0.30$.

e. Ground activity and light intensity

Light intensity is correlated with lunar periodicity and cloud coverage. So is the ground activity of the scorpions. If each month on a lunar calendar were divided into three periods - the pre-full moon; the peri-full moon; and the post-full moon - with equal number of days, and if the luminous intensity of each night was corrected by the cloud cover of the corresponding night, the trapped scorpions of each species can be grouped into the corresponding periods (table 8).

To test the hypothesis that the ground activity of the scorpions depends on light intensity, I did a series of X^2 -tests again. The results show that the ground activities of both *C. exilicauda* and *V. spinigerus* are negatively correlated with the luminous intensity. For *C. exilicauda* $X^2=15.60$, d.f.=2, $p<0.001$; and for *V. spinigerus* $X^2=94.289$, d.f.=2, $p<<0.001$. In contrast, *H. arizonensis*' ground activity is marginally insignificant to light conditions, with $X^2=5.87$, d.f.=2, $p>0.05$.

I have two explanations for the correlations. First, unlike *C. exilicauda* and *V. spinigerus*, *H. arizonensis*' ground activity is only concentrated into a short period of each year. To fulfill the basic requirements for surviving, they have to exploit this precious period more intensively than the others do. Furthermore, the massive body structure of *H. arizonensis* give them predacious advantages over the other scorpions. In other words, both *C. exilicauda* and *V. spinigerus* are more likely to be the victims of intra-guild predation. Second, active foragers may fall victim to nocturnal vertebrate predators that rely on light to hunt. To minimize

Table 8. Trapping frequency of the scorpions in different luminous intensity range.

luminous intensity	scorpions of being trapped		
	pre full moon	full moon	post full moon
species			
<i>C. exilicauda</i>	18	3	24
<i>H. arizonensis</i>	13	4	14
<i>V. spinigerus</i>	86	19	144
young <i>V. spinigerus</i>	30	0	48
adult <i>V. spinigerus</i>	56	19	96

Table 8. Trapping frequency of the scorpions in different luminous intensity range. Data come from the total trapped scorpions in 1991. Moon phase conditions were corrected by the sky coverage data from the "Local Climatological Data" documented by National Oceanic and Atmospheric Administration (NOAA).

the chance of encountering these predators and consequently to lessen the probability of getting killed, *C. exilicauda* and *V. spinigerus* have to restrain their ground activities during bright nights.

2). Daily ground activity pattern

All three species are nocturnal. In general, their ground activities peaked during the first two hours after dawn, and diminished after midnight. Based on my observations from eight night trips, the ground activity pattern varies among the species (figure 11).

Individuals of *C. exilicauda* are active on the ground all through the night. And their ground activity has no significant peaking hour through the night. They are the generalists in utilizing the available time.

In contrast, individuals of *H. arizonensis* emerge from their burrows at 20:00, and return to their burrows around 04:00. Their ground activity peaked from 21:00 to 23:00.

Similar to *H. arizonensis*, individuals of *V. spinigerus* are active on ground surface from 20:00 to 04:00. And their ground activity peaked from 21:00 to 24:00. Thus, the peak period of *V. spinigerus*' activity lasted one hour longer than *H. arizonensis*'.

The daily ground activity patterns of *H. arizonensis* and *V. spinigerus* agree with the pattern shown by some other desert scorpions (Hadley and Williams,

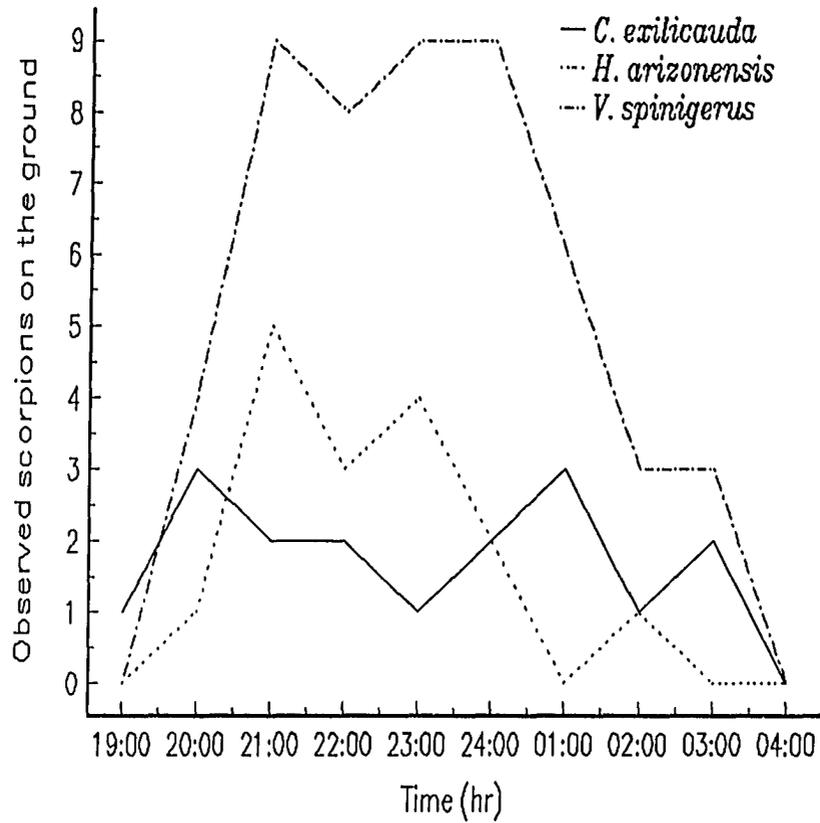


Figure 11. Night ground surface activity of the scorpions. Based on the data collected during eight discrete field trips at night in the study area. Y-axis represents the actual observed scorpions during these field trips.

1968; Shorthouse, 1971; Polis, 1980a; Benton, 1992). But, the pattern for *C. exilicauda* had not been documented before. I have even seen individuals of *C. exilicauda* running on the ground in the early morning hours.

3). Aggregating behavior

Aggregating behavior has been reported for *C. exilicauda*. In winter months, *C. exilicauda* have been found in piles of 20 to 30 individuals (Stahnke 1966, 1971). I did not observe this behavior in my study area although it may be present. But *V. spinigerus*, after heavy rains, did aggregate on a higher ground. One pitfall, for instance, on a pile of dead prickly pear cactus trapped 5 adults of *V. spinigerus* after a heavy thunderstorm in 1991. This was the maximum number of adult scorpions trapped in one pitfall trap within one trap-checking period. After heavy rains, more than one *V. spinigerus* was likely to be trapped in one pitfall. I could not detect any aggregating behavior of the *H. arizonensis*.

4). Water-drinking behavior

It has been observed many times in my study and others (Hadley 1971) that individuals of *C. exilicauda* drink water from a water supply source. In my study area, there is a bathtub buried flush to the ground. SASI people fill the tub with fresh water to support the wildlife in that area. I have seen individuals of *C. exilicauda* gathered around the tub to drink from it after sunset. Once I saw 3 *C.*

exilicauda drinking water there at the same time. I have also observed them drinking in my laboratory. Neither the *H. arizonensis* nor the *V. spinigerus* drink in the field or the laboratory.

Drinking could be explained by the different cuticular permeability of the scorpions. *H. arizonensis* is very much adapted to a desert environment. The cuticular permeability of their integument is extraordinary low (0.031 mg/cm²/hr at 30 °C) (Toolson and Hadley 1977). This low permeability allows individuals of *H. arizonensis* to survive successfully in a extremely dry environment without drinking. Hadley (1970), for instance, showed no significant increase in body weight when dehydrated individuals of *H. arizonensis* were placed on wet sponge strips for 24 hours. In comparison, an adult individual of *C. exilicauda* has a large ratio of body surface/volume and a high cuticular permeability (0.049 mg/cm²/hr at 30 °C) (Toolson and Hadley 1979). Consequently its rate of water loss is higher than that of the other two species. Probably, individuals of *C. exilicauda* need to drink to survive in a hot and dry desert.

5). Burrowing behavior

Burrowing behavior is absent in *C. exilicauda*. Individuals of this species spend most of their time on vegetation. Occasionally they come down to the ground to look for food and mates or to move to a better plant.

Adults of *H. arizonensis*, however, build their own burrows. They also

accept the abandoned burrows of lizards and rodents.

Burrows belong to one individual. One female *H. arizonensis*, for instance, has been observed using the same burrow for two years in my study area.

The typical burrows in my study area are 50 to 75 cm in depth, but could reach 200 cm in other locations (Stahnke 1966; Anderson 1975). I excavated two burrows of *H. arizonensis* in my study area. Both of them spiraled down forming an arching pathway.

True burrowing behavior in *V. spinigerus* is seldom observed in the field. A simple run under a rock or a shallow burrow against a rock are the common dwellings of this species. But adult individuals are perfectly capable of digging a shallow burrow. I have observed an adult *V. spinigerus* constructing a simple burrows on the bottom sand layer of a terrarium in the laboratory. In the field, large rocks and debris of dead plants are the preferred shelters of *V. spinigerus*.

6). Diet

Scorpions eat almost all creatures they can subdue. The optimal prey size is about the length of the scorpion's pedipalp (Francke 1979). Usually, they prefer live prey, but, in captivity, they consume dead food items and fresh red meat as well (Vachon 1953; Bücherl 1971; Krapf 1986).

Because of their large body size, *H. arizonensis* has a quite broad diet. These include Araneae, Scorpiones, Solifuges, Orthoptera, Coleoptera,

Hymenoptera, Lepidoptera (see Polis 1990 for refs.), and small whiptail lizard (*Cnemidophorus* sp.) (Stahnke 1966). In addition to this list, I observed that a baby lesser earless lizard (*Holbrookia maculata*), a banded gecko (*Coleonyx variegatus*) and a small rodent were also eaten by *H. arizonensis* in the pitfalls. Other species of scorpions, if measured by item count, can comprise as high as 21.9% of their diet (Polis and Yamashita, 1991). This percentage would be much higher if the prey items were measured in biomass.

Diet of the scorpions was not involved in my field work. Instead, I conducted a series of laboratory pilot experiments to test 1) the diet preferences of adult *H. arizonensis* on the size and species of their prey; and 2) the correlation between tolerance of food shortage and the occurrence of cannibalism in *V. spinigerus*.

In the first part of the experiments, I kept four adults of *H. arizonensis* separately in 4 empty 3bl coffee cans (15.5 cm in diameter and 17.5 cm in height). Each of the cans was simultaneously supplied with one adult *V. spinigerus*, one 4 cm long horned tobacco worm (*Manduca sexta*), and one adult house cricket (*Acheta domesticus*). I supplied these live food items to the *H. arizonensis* once a month for four months. The results are in table 9. The *H. arizonensis* ate the *V. spinigerus* as their first prey item 69% of the times, the *Manduca sexta* 25%, and the house cricket 6% of the time. Therefore, captive *H. arizonensis* significantly ($X^2=62.66$, d.f.=2, $p<<0.001$) prefer to eat *V. spinigerus*.

Table 9. Diet preference of *H. arizonensis* in captivity.

time (month)	1	2	3	4
experiment duplication (can #)				
1	V	M	V	V
2	V	V	A	V
3	M	V	V	M
4	V	V	M	V

Table 9. Diet preference of *H. arizonensis* in captivity. The tabulated symbols represent the first prey item of the three possibilities that is killed and consumed by each individual *H. arizonensis* in the experimental replications. V = *V. spinigerus*; M = *M. sexta*; A = *A. domesticus*.

In the second laboratory experiment, three pairs of adult *V. spinigerus* were kept in three number 3 cylinder cans. I provided the scorpions with water, but no food for three months. I kept a fourth control pair of *V. spinigerus* in the same conditions, but gave them water and food biweekly. By the end of the experiment, the *V. spinigerus* in the control were still alive. However, four of the six *V. spinigerus* in the experimental cans had died during the study. Strikingly, no cannibalistic behavior was observed. Perhaps the body sizes of the paired *V. spinigerus* were not different enough to let them prey upon one another, or perhaps, the *V. spinigerus* do not cannibalize at all.

In addition to the laboratory result, I never saw a single case of cannibalism between individuals of *V. spinigerus* inside the pitfall traps, even though quite often more than two *V. spinigerus*, sometimes differing much in body size, were trapped in the same pitfall trap for 3.5 days on average. I have often seen that *H. arizonensis* prey on adults of *C. exilicauda* and *V. spinigerus*, if they happened to be trapped in the same pitfall trap. Predation between adult *C. exilicauda* and adult *V. spinigerus* were also not seen inside the pitfall traps. But they did occur in both directions in laboratory captivity. In all of the observed predation cases, who eats who is completely determined by the body sizes of the scorpions involved. In my study area, the most frequently observed intra-guild predation was performed by adult *C. exilicauda* preying on young *V. spinigerus*.

7). Foraging tactics and travelling distance

The burrowing scorpion, *H. arizonensis*, is a sit-and-wait forager. After dawn, they emerge from their burrows and wait motionlessly on the ground for approaching prey. Among the 16 *H. arizonensis* I have spotted by using a UV light during my night trips, only one of them was traveling.

Prey items are detected by ground vibration sent off by passing insects. Detection is facilitated by a pair of unique comb-like appendages (pectines), located ventrally on the metasoma. Polis (1990), worked with another large desert species in North America, the desert sand scorpions *Paruroctonus mesaensis* at Riverside county, California, and estimated that the range of prey detection was about 50 cm for adult *P. mesaensis*.

For adults of *H. arizonensis*, which are larger than adult *P. mesaensis* (Polis and McCormick, 1986, 1987), the prey detecting range is probably greater than 50 cm. I have seen one gravid female *H. arizonensis*, in one of the study sites, feed on a prey item two meters away from its burrow. Usually, captured prey are consumed where they were captured.

Individuals of *H. arizonensis* rarely change their foraging sites except during the mating season. The travelling distance calculated from 7 recaptured *H. arizonensis* was 10.97 ± 7.12 (mean \pm se) meters per week per individual. The maximum distance traveled, in one week, by a *H. arizonensis* during the study period of 1991 was 45.83 meters.

Adults of *C. exilicauda*, the arboreal species, spend some of their foraging hours traveling on the ground. The travelling distance calculated from 15 recaptured *C. exilicauda* in 1991 was 10.65 ± 2.75 (mean \pm se) meters per week per individual. The maximum distance traveled by a *C. exilicauda* in one week was 36.46 meters.

I have seen individuals of *C. exilicauda* chasing their prey on the ground. Successful capture can take place either on the ground or on vegetation. But ingestion is mainly done on a nearby bush or tree. I have observed many times an adult *C. exilicauda* dragging its prey into a nearby bush to consume it there. This behavior has also been observed many times in other species of scorpions with a small body size, and in the younger age groups of large species (Hadley and Williams, 1968; Polis, 1979; Polis and McCormick, 1986).

Prey consumption in the open ground has never been observed for *C. exilicauda* during my study period. It usually takes 1 to 3 hours for an adult *C. exilicauda* to finish eating a medium sized prey in the laboratory. I believe they drag their prey into vegetation to avoid predation themselves.

The foraging tactics adopted by *V. spinigerus* is intermediate between those of *H. arizonensis* and *C. exilicauda*. Individual *V. spinigerus* use both sit-and-wait and moving-around tactics during foraging. They also chase their prey on the ground. I have seen a few times of this chasing game in my study area. Individuals of this species may consume the captured prey where captured or first

they may drag the prey into a nearby bush. The travelling distance calculated from 67 recaptured *V. spinigerus* was 19.28 ± 2.36 (mean \pm se) meters per week per individual. The maximum distance traveled by a *V. spinigerus* during the study period was 80 meters in one week.

8). Microhabitat use

Individuals of *C. exilicauda* are most likely to be found in relatively moist places, such as underneath the dead bark of big trees, the petioles of palm trees, and underneath large rocks. *V. spinigerus* is more abundant in rocky areas than in other habitats. This has been demonstrated in my study area and in the area studied by Williams (1970) in Phoenix' South Mountain. Most often, individuals of *V. spinigerus* will use large rocks, fallen trees and dead cacti as shelters. In contrast, individuals of *H. arizonensis* prefer a dry and fine substrate habitat that is not too flat. The choice of fine substrate may be related to their burrowing behavior.

In the following two chapters I will discuss both habitat use and habitat selection of the scorpions in detail.

CHAPTER 3. HABITATS AND THEIR USE.

A. THE HABITATS

1). Definitions and descriptions

Habitat changes occur in both time and in space. Usually, it is difficult to distinguish the population dynamics caused by temporal habitat change from those caused by change of population density. This could raise serious problems when density-dependent habitat selection is the major concern. To avoid as much temporal variation as possible, I have chosen four relatively constant habitat dimensions to work with. The four dimensions are: vegetation coverage; substrate fineness; ground level; and the size of the rocks I selected to cover the pitfall traps.

I separated each of the habitat dimensions into two categories. "Open" and "covered", for instance, are for the dimension of vegetation coverage; "fine" and "coarse" are for the dimension of substrate fineness; "high" and "low" for the ground level; "large-rock" and "small-rock" for the rock size. I refer to each of these categories as a habitat property.

Each pair of habitat properties on the same habitat dimension is mutually exclusive by definition. That is, a particular habitat cannot be both open and covered simultaneously. Nor can a habitat have neither property. But habitat

properties from different dimension must overlap. For instance, a place could be open, fine, high and large rock at the same time.

Each pitfall trap in my study area thus represents a habitat with four properties. Because of the patchy nature in each habitat dimension, two different pitfall traps are rarely identical on all of the four dimensions.

Here are the definitions of the properties. "Covered" stands for a habitat or a pitfall trap that is placed under plant foliage; "open" is the reverse of "covered". "Fine" stands for a habitat where the soil particles are relatively fine (<5 mm in the longest dimension); the soil particles in "coarse" habitat exceed 5 mm in the longest dimension. A "high" habitat stands above the surface 1 m around it; and a "low" habitat is lower compared with the surface 1 m around it. A "large-rock" habitat represents a pitfall trap that is covered by a large (>16 cm in the longest dimension) sized rock; and "small-rock" stands for relatively small (≤ 16 cm in the longest dimension, but still covers the pitfall trap perfectly) cover rock of the pitfall traps.

In addition to limiting the temporal elements, I choose these habitat dimensions based on the following concerns: 1) the scorpions' lifestyle - arboreal vs. ground; 2) the scorpions' burrowing behavior - burrowing vs. non-burrowing. In fact, I was planning to investigate three habitat dimensions at the beginning of my experiment. The ground level dimension was added to my study only after I noticed that during heavy rains, water had accumulated in those pitfall traps

buried in lower places, and many scorpions were drowned in those pitfall traps. Therefore, I wondered if ground level could be an influential habitat dimension for the scorpions.

2). Independence of the habitat dimensions

To eliminate as much complexity as possible, I used two criteria to select the points where the pitfall traps were located. 1) Within each study site, the ratio of each pair of mutually exclusive habitat types should be close to one. 2) Between the study sites, the proportion of each habitat type of the four dimension should be similar. I have tabulated the final design of those habitats in table 10.

Combining the habitat types from each of the four habitat dimensions, I have, theoretically, sixteen possibilities. If the habitat dimensions are independent of one another, then the forty-five pitfall traps or habitats should be evenly distributed among the sixteen possibilities. To check for independence, I used the Kolmogorov-Smirnov one-sample test. My working hypothesis was: the occurrence of combinations among the four habitat dimensions is uniform. At a 5% significance level and a sample size of 45, the critical value is 0.179. The test statistic is $0.088 < 0.179$. Thus, I conclude that the four habitat dimensions are independent with one another.

In addition, I did a cluster analysis on the same data set of habitat dimensions. The result agrees with the one from Kolmogorov-Smirnov one-

Table 10. Habitat types in each of the study sites.

study site	habitat dimensions							
	vegetation		substrate		rock-size		ground-level	
	covered	open	coarse	fine	small	large	low	high
A	8	7	7	8	7	8	8	7
B	8	7	6	9	7	8	8	7
C	8	7	9	6	7	8	7	8
total	24	21	23	22	21	24	23	22

Table 10. Habitat types in each of the study sites. For instance, there are 8 covered and 7 open habitats in all three sites; 7 coarse and 8 fine habitats in site A, but 6 coarse and 9 fine in site B.

sample test above (figure 12).

B. GENERAL RESULTS OF HABITAT USE

Recall that a scorpion's body size determines who wins a predator-prey encounter. Here, I further assume that large scorpions always have an advantage over the small ones in interference competition. I also assume that large scorpions always have a broader diet. These assumptions ensure the advantage of large scorpions in competition. Granted the existence of strong interactions among the scorpion populations, habitat use of the small scorpions should depend on the habitat use of the large species.

Williams (1968) has found that pitfall traps which were covered by rocks, captured a significantly greater number of scorpions than those without rocks. During my field work, I kept the pitfall traps covered by selected rocks all the time.

If a scorpion happened to be trapped in a pitfall classified as covered, fine, large, and low, then I considered that the covered, the fine, the large, and the low habitats have been used simultaneously once by that particular scorpion. Because each pair of habitat properties on each dimension are mutually exclusive, the in percentage use is complementary. For instance, if 45% of the individuals of *H. arizonensis* uses the covered habitat in study site A, then 55% of the same species

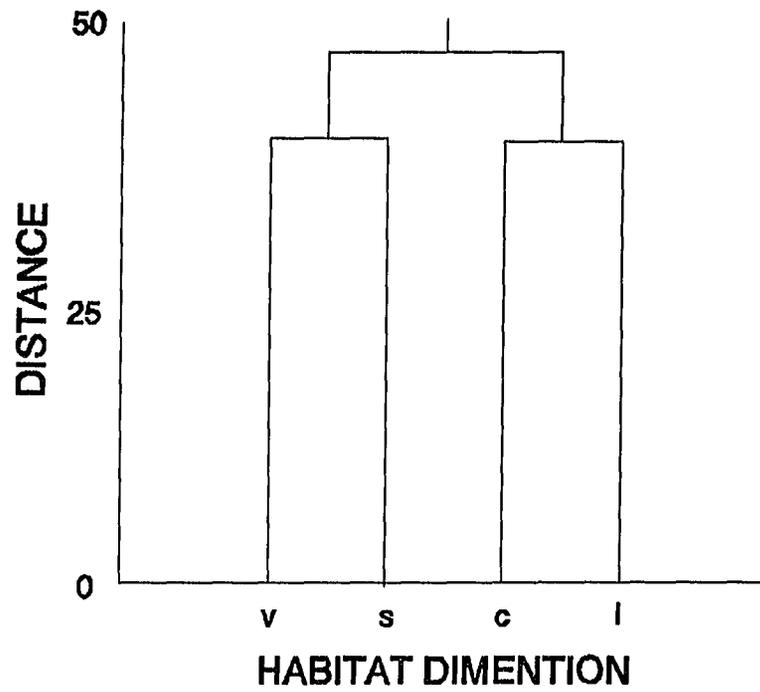


Figure 12. Tree diagram of cluster analysis of the habitat dimensions. Distance metric is normalized percent disagreement. Nearest neighbour linkage is used. v = vegetation coverage; s = substrate fineness; c = size of cover rock; l = ground level.

must have used the open habitat in the same study site.

I define a preferred habitat property as the one used more often by a particular species of scorpion when the density of all scorpion species is relatively low. But, I will not discuss the scorpions' population densities in this chapter. So, I have to assume in this chapter that population sizes do not matter. In the next chapter I will relax this assumption. I postulate the preferences based on the scorpions' behaviors and their percentages of habitat use: 1) *C. exilicauda* prefers the open, fine, low, and large-rock habitats; 2) *H. arizonensis* prefers the open, fine, low, and small-rock habitats; and 3) *V. spinigerus* prefers the open and large-rock habitat properties; they show no preference for the other habitat dimensions.

Because of the complementary nature of the percentage use of habitat types, I will, for convenience, consider only one of them from each habitat dimension in the following discussions.

I have tabulated the percentages of habitat use for each species from each study site in table 11, and the total captures of scorpions in table 12. All the data in these tables came from the census data I collected in the field during 1991. The following discussion mostly depends on the information of these two tables.

1). *C. exilicauda*

C. exilicauda, in study site A - the site with the highest scorpion density,

Table 11. Percentages of habitat use for the scorpions in all of the study sites.

<i>C. exilicauda</i>				
habitat	study site			
dimension	A	B	C	all sites
vegetation (covered)	42.9%	41.2%	78.6%*	53.5%
substrate (coarse)	21.4%*	29.4%	85.7%*	44.4%
rock size (small)	57.1%	52.9%	28.6%*	46.7%
ground level (low)	42.9%	58.8%	28.6%	44.4%
<i>H. arizonensis</i>				
habitat	study site			
dimension	A	B	C	all sites
vegetation (covered)	25.0%	11.1%	83.3%*	32.3%
substrate (coarse)	25.0%	22.2%	33.3%	25.8%
rock size (small)	81.3%	55.6%	16.7%*	61.3%
ground level (low)	75.0%*	22.2%*	00.0%*	45.2%
<i>V. spinigerus</i>				
habitat	study site			
dimension	A	B	C	all sites
vegetation (covered)	63.0%	45.3%	58.5%	56.2%
substrate (coarse)	52.2%	46.7%	61.0%	54.4%
rock size (small)	31.5%	28.0%	26.8%	28.9%
ground level (low)	56.5%	38.7%	36.6%	44.6%

Table 11. Percentages of habitat use for the scorpions in all of the three study sites. For those marked by the * are significant from the corresponding percentage of all sites when I used a series of pair-wise X^2 -test at 5% significant level with d.f.=1. All the rest percentages are insignificant when the same test applied.

Table 12. The total captures of scorpions in 1991.

species	<i>C.exilicauda</i>	<i>H.arizonensis</i>	<i>V.spinigerus</i>	sum
study site				
A	14	16	92	122
B	17	9	75	101
C	14	6	82	102
total	45	31	249	325

Table 12. The total captures of scorpions in the three study site in 1991, including recaptured, dead, and young *Vaejovis spinigerus*.

uses significantly more fine substrate habitats than the average taken from the three study sites ($X^2=8.21$, d.f.=1, $\alpha=0.05$). I think the following explains what was happening in site A. Individuals of *H. arizonensis*, the burrowing species, needs fine substrate to dig their burrows. And burrowing behavior is important for their survival. Therefore, they should prefer fine substrate. In fact they did (see table 11). By contrast, both *C. exilicauda*, the arboreal species, and *V. spinigerus*, the vagrant species, do not dig their own burrows. Thus, substrate should not much concern them. These are shown in table 11. So what might happen is the following. When the densities of both *H. arizonensis* and *V. spinigerus* are high, these two species differentiate their substrate use - the fine for *H. arizonensis* and the coarse for *V. spinigerus*. In this scenario, the individuals of *C. exilicauda* face the dilemma: where to go? Within fine substrate habitats, they have to suffer the competition or possibly predation from the giant *H. arizonensis*. Within coarse substrate habitats, on the other hand, they also have to suffer the competition and possibly predation from the numerous *V. spinigerus*. Two key facts hold the answer the this question. First, exploitative competition is stronger between the individuals of *V. spinigerus* and *C. exilicauda* because they are more similar in body size, and consume similarly sized prey items. Second, *V. spinigerus* is about five times more abundant than *H. arizonensis* in site A. And this will strengthen the competition between *V. spinigerus* and *C. exilicauda* even further. Thus, if the concerning population interaction is the paramount force to control

the scorpions' behaviors, then, individuals of *C. exilicauda* should avoid competing with *V. spinigerus* and use the fine substrate habitats more often. This is what actually happened in site A. And the simple X^2 -test shown this. In the fine substrate habitats *H. arizonensis* and *C. exilicauda* could coexist by using different habitat dimensions - the ground for the giant hairy and the vegetation for the bark scorpions. Then, why the *C. exilicauda* would not use the coarse substrate with *V. spinigerus* and differentiate on the ground and plant dimensions? The answer relies on the potential plant-climbing ability of *V. spinigerus*. But this ability is either completely absent or rarely used in *H. arizonensis*.

Thus at high densities of both *H. arizonensis* and *V. spinigerus*, *C. exilicauda* tends to coexist with *H. arizonensis* on the fine substrate habitats by differentiating on another niche axis, which they could not effectively do with *V. spinigerus*.

Scorpions were less abundant in study site C. In this site, *C. exilicauda* use significantly more the covered habitats ($X^2=4.88$, d.f.=1, $\alpha=0.05$), significantly more the coarse substrate habitats ($X^2=13.34$, d.f.=1, $\alpha=0.05$), and significantly more the large rock habitats ($X^2=4.39$, d.f.=1, $\alpha=0.05$). It seems the bark scorpions switched a great deal of their habitat preference to the opposites in site C.

I try to explain these switching phenomena by first assuming that for *H. arizonensis* the study site C is a poorer site in resources (food, mate, and high predation pressure etc.) than the other study sites are. If this is true, then the

individuals of *H. arizonensis* will behave differently in this site. They would perform one of the following two actions. First, they could lose their habitat preference and consequently show a random pattern on habitat use. This probably indicates a shortage of mates at low population density. Second, they could switch their habitat preference to the opposite directions. This probably indicates a shortage of food at a poor site. What happened in site C, I think, is that the *H. arizonensis* switched its habitat preferences to the opposite because of food shortage. The data in table 11 demonstrate these switches.

In desert environment the major group of scorpions' food items is associated with vegetation. This is especially true when the food items are scarce. If food is in short supply, *H. arizonensis* will switch from their more preferred habitats into the less preferred ones. For instance, the individuals of *H. arizonensis* will switch to the covered habitats to look for the less profitable and plant associated small insects or scorpions as food. Consequently, the switching of habitat preference will force more individuals of *V. spinigerus* to use the open habitats in site C. Therefore, the density of *V. spinigerus* in the open habitats will increase; and the density of *H. arizonensis* in the covered habitats will decline. In the open habitats *C. exilicauda* have to compete with or be hunted by both *V. spinigerus* and *H. arizonensis*. However, in the covered habitats, *C. exilicauda* still have to compete with both of the competing species, but the only predator they have to face with is the *V. spinigerus*, if they use plants as refuge. Furthermore,

C. exilicauda has an advantage over *V. spinigerus* on the vegetated habitat.

Thus, the predation risk and competition pressure on *C. exilicauda* are reduced if they use more vegetated habitat whenever individuals of *H. arizonensis* switch their preference for the open habitat to the covered ones.

Use the same argument as above. If *H. arizonensis* use more coarse substrate in site C, actually they do, (see table 4), consequently more *V. spinigerus* will use relatively more fine substrate habitat. The *V. spinigerus* in the fine substrate will force the *C. exilicauda* to use more coarse substrate. This is because *C. exilicauda* and *V. spinigerus* share more similarities to compete the same habitat than *C. exilicauda* and *H. arizonensis* do. Thus, when *H. arizonensis* increase their use on coarse substrate, *C. exilicauda* will increase their coarse substrate use as well.

By the same argument, when individuals of *H. arizonensis* switch their preference to use more large rocks (see table 11), *C. exilicauda* will also use more large rocks.

All in all, *H. arizonensis* behaves as a protector of *C. exilicauda* when *V. spinigerus* is more abundant. From the information of habitat use in *H. arizonensis*, and the density of *V. spinigerus* we might predict the habitat use of *C. exilicauda*. The preference changes are active for *H. arizonensis*, and passive for *C. exilicauda*. In other words, *H. arizonensis* behaves in the way to fulfill its own interests, but *C. exilicauda* has to adjust its behavior by watching the others'

doings. *H. arizonensis*' motive of switching its habitat preferences probably correlated with food shortage rather than mate shortage. Two facts will support this. First, no sexual dimorphism in *H. arizonensis*, and both males and females prefer the same habitats. So, in the preferred habitats mates are probably easy to find. Second, the courtship of this species could be triggered by either sex. So, they should be randomly distributed among the habitats if mates were really in shortage. For *C. exilicauda*, the pressures of competition and possibly predation from *V. spinigerus* is stronger than the same pressures from *H. arizonensis*. Again, the scorpions' body size, abundance and behavior are responsible for this result.

2). *H. arizonensis*

Individuals of *H. arizonensis* prefer the open habitats, low ground level habitats, and the small rock habitats in general (see next chapter). But all these preferences switch to their opposites in study site C. I have explained this in the preceding section. There, I concluded that the habitat preference switching in *H. arizonensis* was due to food shortage in site C. Here, I try to make another related point, but only briefly.

It will be interesting to know whether interguild predation for the *H. arizonensis* composes the major part of its diet regime. In other words, do the giant hairy scorpions mainly rely on the other small scorpions for their food. The answer is that they do not.

Suppose that the individuals of *H. arizonensis* in my study area do mainly depend on the other small scorpions as food supply. Then I should expect that the densities of both *C. exilicauda* and *V. spinigerus* would be significantly lower in site C than in the other sites. Because only in site C the individuals of *H. arizonensis* switched their habitat preference to the opposite directions. But this was not the case. In fact, the density of *V. spinigerus* and *C. exilicauda* in site C did not significantly differ from the other sites (see table 12). Thus, the supposition was incorrect. I think the role played by *H. arizonensis* to the other scorpions is mostly a competitor rather than a predator.

Individuals of *H. arizonensis* prefer the fine substrate habitats through all study sites. Fine substrate let them build their burrows more easily.

3). *V. spinigerus*

Individuals of *V. spinigerus* showed weak preference on the covered habitat, and no habitat preferences between the coarse and fine substrate habitats, and between the low and high ground level habitats. To test the significance of habitat preference of *V. spinigerus*, I have done a series of pairwise X^2 -tests. My hypothesis was that the percentage of habitat use from all sites is statistically the same as the percentage of the corresponding habitat use from any particular study site. All the X^2 -test statistics were insignificant at 5% significant level with a degree of freedom of one.

However, individuals of this species showed consistent preference for large rock habitats along the study sites. A X^2 -test combining the three study sites resulted a $X^2=0.410$. At 5% significant level and with a degree of freedom of two, the result is insignificant. This confirms that the striped tail scorpions consistently prefer the large-rock habitat in all the study sites.

Large rocks protect *V. spinigerus* from natural predators and from extreme weather conditions. And such protection could be crucial for the scorpions' survival.

C. DISCUSSIONS

So far, I have discussed habitat use of the three species of scorpions in general. All of these discussions are based on the calculated percentages of habitat use in each study site for each species. To carry on these discussions, I have made some necessary assumptions. As I have pointed out, knowing the preferred habitats is quite elusive without first understanding the scorpions' population dynamics and the associated behaviors. But the more fundamental question should be: if the scorpions really have habitat preferences. Or simply, do they really choose? This is certainly not as a simple question as it seems to be.

By looking at the data in table 11, I can make two concrete conclusions about the scorpions' habitat use. First, individuals of *H. arizonensis* consistently used a significantly large percentage of the fine substrate habitats among the three

study sites. I have done two separate X^2 -tests to show this result. I called the first X^2 -test the test of consistency, and the second test the test of preference. To test the consistency of fine substrate use among the study sites, I did the first X^2 -test on the percentages from the study sites. At 5% significant level and a degree of freedom of 2, the critical X^2 value is 5.991; and the calculated statistic is 2.425. Thus, I have to accept my working hypothesis: Individuals of *H. arizonensis* in different study sites used the same percent of fine substrate habitats. In the second X^2 -test, I tried to answer the question: Do the individuals of *H. arizonensis* really prefer the fine substrate habitats? If they do, then the average percent of fine substrate habitats used by *H. arizonensis* taken from all the study sites should differ statistically from the percent of the existing fine substrate habitats in the study sites. The calculated statistic is 8.480, which is greater than the critical X^2 value 3.841. At 5% significant level and a degree of freedom of 1, the result is significant. Thus, I reached my first conclusion: Individuals of *H. arizonensis* consistently used a significantly large percentage of the fine substrate habitats among the three study sites.

My second conclusion is that individuals of *V. spinigerus* consistently used significantly more of the large rock habitats among the three study sites. Using the same technique and reasoning, I did another two X^2 -tests. The consistency test resulted in an insignificant statistic ($X^2=0.410$, d.f.=2, $p>0.80$). This supports the hypothesis that individuals of *V. spinigerus* in different study sites used the

same percent of large rock habitats. The preference test resulted in a significant statistic ($X^2=4.230$, d.f.=1, $p<0.05$). This reveals that *V. spinigerus* do prefer large rock habitats. Summing up the results from these X^2 -tests, I concluded that individuals of *V. spinigerus* consistently preferred the large rock habitats among the three study sites.

By now, I am a little more confident in saying that scorpions do have their habitat preferences. They choose! It is those choices made by individual scorpions that characterize those critical ecological features that show up at the population and community levels.

Unfortunately, the choices made by the scorpions are not constant. And this is especially true when density-dependent habitat selection is the main concern. To pursue this concern, I must apply another analytic technique to relate scorpions' individual choice to their population dynamics. Isoleg analysis (Rosenzweig 1987, 1990) does more than that. Applying the isoleg model to my data is the task of the next chapter.

CHAPTER 4. ISOLEG ANALYSIS OF HABITAT USE.

A. INTRODUCTION

Isoleg analysis is a set of graphical theories of density-dependent habitat selections. An isoleg is a threshold dividing a species' disjunct behaviors in a density state-space. The shape of the threshold is not so important, but its slope is crucial. From the slope of the thresholds, one can understand the type of preference and the organization of the system.

During the last decade, isoleg analysis has allowed the study of habitat selection of hummingbird (Rosenzweig, 1986), of desert rodents (Abramsky, Rosenzweig etc., 1990, Brown 1986), and of bumblebees (Rosenzweig, unpubl.). All these works have showed the robustness of isoleg analysis in detecting the pattern of community organization. Yet, the theory behind the isoleg model is still growing and expanding. More experiments need be done to test its generality.

One important aspect of isoleg analysis is the combination of individuals' behavior and population density to study the ecological community. At its current stage of development, isoleg models come from three kinds of community organization (Rosenzweig, 1989). The distinct-preference best explains the Ghost of Competition Past. The shared-preference best explains the community organization if resource varies. The centrifugal-preference, taking the shared-preference at the primary level and the distinct-preference at the secondary level,

best explains the phenomenon of reverse niche shift.

In my field work, I have sampled the densities of the three population of scorpions. In addition, I have recorded the frequency of habitat use as well. So, my data is appropriate for isolog analysis.

B. DATA ANALYSIS

1). Assumptions

To apply isolog analysis, I have pooled the data from the three study sites. In doing this, I assume that the trapped scorpion samples in each site proportionally represent the true scorpion populations. Further, I assume that the scorpion composition is similar across the study sites. Two other reasons allowed me to pool the data. First, the population densities of each species are not significantly different among the three study sites (table 13). The X^2 value is 0.400 for *C. exilicauda*, 5.097 for *H. arizonensis*, and 0.759 for *V. spinigerus*. At 5% significance level with a degree of freedom equals 2, all the results are not statistically significant.

Secondly, if all the trapped scorpions from the three species are combined in each study site, the scorpions' overall habitat use is not significantly different for each site (table 14). I Conducted a X^2 -test for each habitat type of each site against the corresponding average habitat use. All the results are statistically

Table 13. Number of scorpions captured in each study site.

species	<i>C. exilicauda</i>	<i>H. arizonensis</i>	<i>V. spinigerus</i>
site			
A	14	16	92
B	17	9	75
C	14	6	82

Table 13. The number captures of scorpions in the three study site in 1991, including recaptured, dead, and young *Vaejovis spinigerus*.

Table 14. Habitat use percentage in each study site.

site	A	B	C	Average
habitat type				
vegetated cover	55.7%	41.6%	62.7%	53.5%
coarse substrate	45.1%	41.6%	62.7%	49.5%
small rock size	41.0%	34.7%	26.5%	34.5%
low ground level	57.4%	40.6%	33.3%	44.6%

Table 14. Percentages of habitat use after pooling the data of three species of scorpions in each study site.

nonsignificant at 5% significance level with a degree of freedom equals 1.

In addition, I designed the study sites to be the same size and have the same combination of habitat types. And I set up the same number of pit-fall traps in each site.

2). Data transformation

a. Polynomial regression

During 1991, I checked the pitfall traps at various intervals. When the project started, I had no idea how successfully the traps would function. So I went to the field as often as I could to avoid unnecessary mortality of the trapped scorpions. I checked the traps once every two days in May; twice a week from June to the middle of October; and once each week thereafter. Altogether, I spent forty-seven early mornings in the field to check the pitfall traps in that year.

Even though a total of 325 scorpions were trapped in 1991, most (74%) of them belong to one species (*V. spinigerus*). Thus, the trapping data for the other two species were sporadically distributed along the sampling period. This hampers my analysis on population density and habitat use. To overcome the problem I reorganized the data in the following way.

Using seven days as a basic sampling unit, I reorganized the total trapping data into 26 units or periods. One individual, regardless of how many times it was trapped in a period, was counted only once for that period. The result is in table

15.

Because of the infrequent ground activity of the scorpions, this reorganized distribution of trapped scorpions still shows irregular behavior. To smooth the data distributions, I added four adjacent week's data together, and assigned the result to the third week. This addition has been done separately for each species. To parallel this transformation, I simply multiply the first and the last weeks' data by three. The second week's data takes the first two weeks' average and is multiplied by three. The results are listed in table 16.

There are two reasons to transform the data tails. I do not want to lose three data points for each species. Each data point is precious for the isoleg analysis. More data will enhance its reliability. Second, it seems logical to multiply these tail data by a magnitude of fourfold. But in reality the scorpions are scarcer on the ground surface during those out of season periods. If I extrapolated the density distribution of the scorpion along the sampling period, I would most likely capture no scorpion at the beginning or the end. The declining trend of the scorpions' densities allowed me to multiply the tail data by three not four.

I have fit the data in this table to a 4th order polynomial for each species of scorpion (see figures 13, 14, 15 and table 17). This yields three equations estimating the population dynamics during my sampling period. I have tabulated the estimated population sizes for each species in table 18. My analysis depends

Table 15. Weekly distribution of the captures.

week	day	total captures			recapture and young w/in week		
		C	H	V	C	H	V
0	05/05/91	2	0	3	1	0	1
1	05/12/91	3	0	2	0	0	0
2	05/19/91	2	0	3	1	0	0
3	05/26/91	2	0	1	0	0	0
4	06/02/91	0	0	11	0	0	2
5	06/09/91	3	0	3	1	0	0
6	06/16/91	2	1	3	0	0	0
7	06/23/91	3	0	5	0	0	0
8	06/30/91	2	1	6	0	0	0
9	07/07/91	5	2	19	0	0	5
10	07/14/91	2	4	9	0	0	3
11	07/21/91	1	2	7	0	0	1
12	07/28/91	0	6	6	0	0	1
13	08/04/91	2	2	15	0	0	6
14	08/11/91	7	1	13	0	0	3
15	08/18/91	1	2	11	0	0	2
16	08/25/91	2	0	18	0	0	9
17	09/01/91	0	0	15	0	0	5
18	09/08/91	0	2	18	0	0	3
19	09/15/91	3	1	16	0	0	1
20	09/22/91	0	2	18	0	0	10
21	09/29/91	0	2	15	0	0	7
22	10/06/91	1	0	11	0	0	7
23	10/13/91	1	1	12	0	0	10
24	10/20/91	1	1	5	0	0	4
25	10/27/91	0	1	4	0	0	3

Table 15. The distribution of the captured scorpions reorganized among the 26 weeks. C is for *C. exilicauda*; H is for *H. arizonensis*; and V is for *V. spinigerus*.

Table 16. Number of captures from each four adjacent sampling weeks.

week	<i>C. exilicauda</i>	<i>H. arizonensis</i>	<i>V. spinigerus</i>
0	3	0	6
1	6	0	8
2	7	0	9
3	6	0	16
4	5	0	16
5	6	1	16
6	7	1	20
7	9	2	17
8	12	4	28
9	12	7	31
10	10	9	32
11	8	14	31
12	5	14	26
13	10	11	30
14	10	11	33
15	12	5	37
16	10	3	38
17	3	4	43
18	5	3	49
19	3	5	48
20	3	7	46
21	4	5	35
22	2	5	22
23	3	4	15
24	3	3	8
25	0	3	3

Table 16. Summation of three adjacent week's captures. These data are used for the fourth order of polynomial regression.

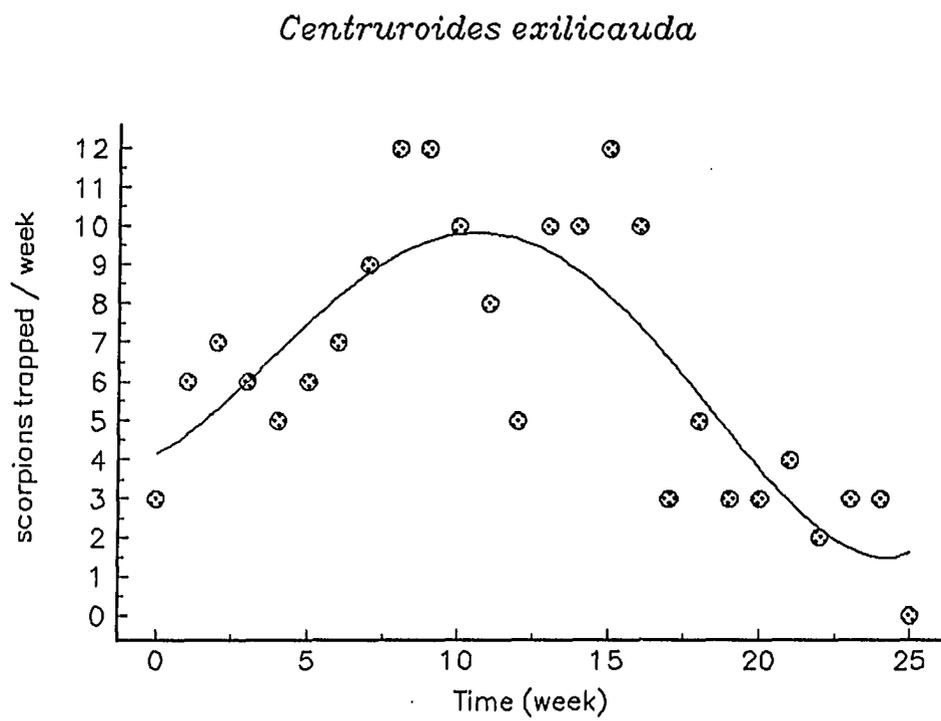


Figure 13. The fourth order of polynomial regression.

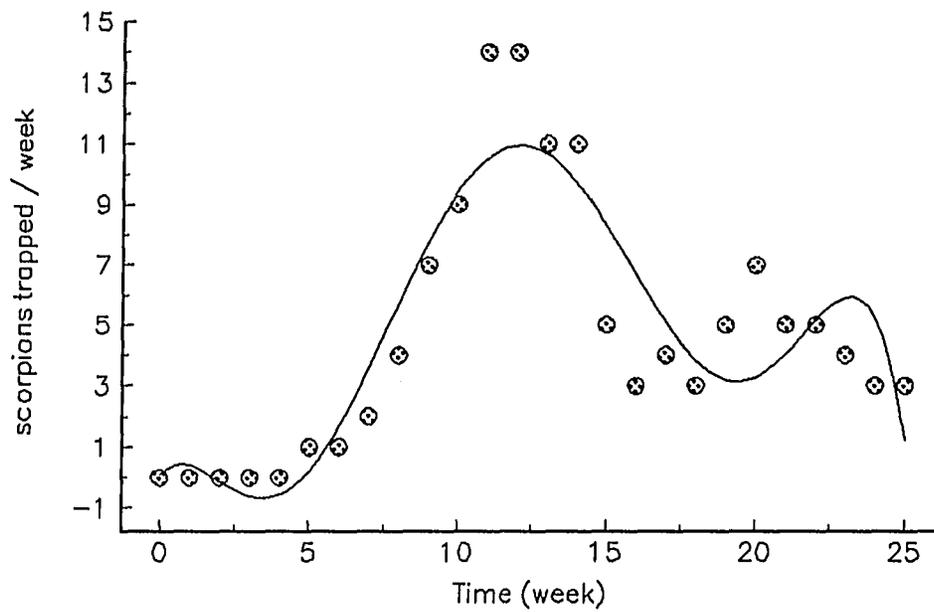
Hadrurus arizonensis

Figure 14. The fourth order of polynomial regression.

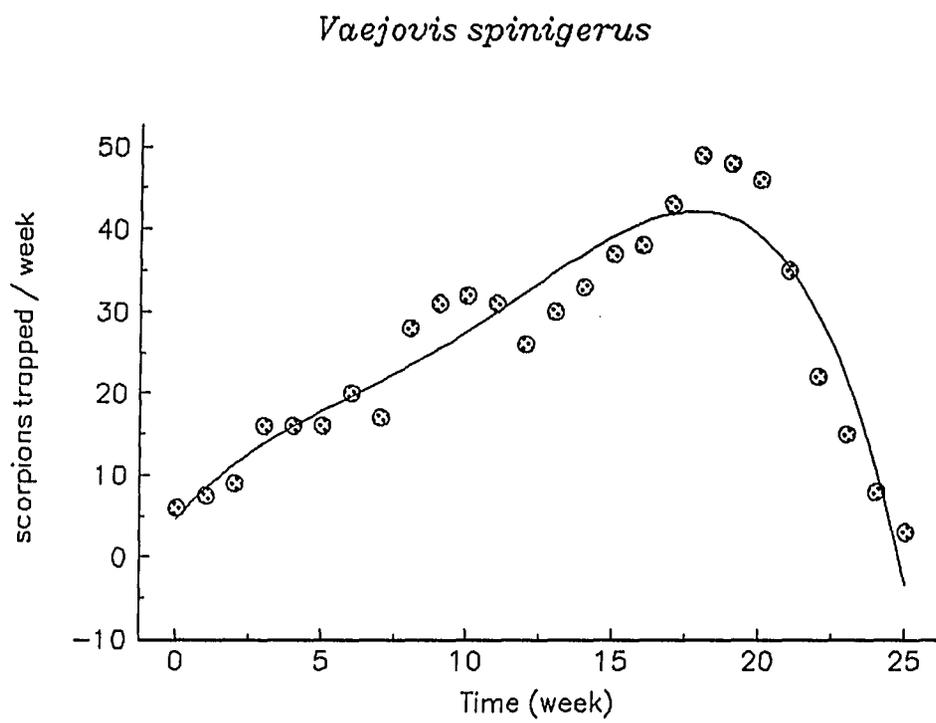


Figure 15. The fourth order of polynomial regression.

Table 17. The statistics from the fourth order of polynomial regression on each of the scorpion species.

Centruroides exilicauda

Parameter	Final estimate	Standard dev.	t	Prob(t)
c0	3.03242	1.45934	2.08	0.04959
c1	1.03071	0.93052	1.11	0.27997
c2	0.0124613	0.16426	0.08	0.94021
c3	-0.00645007	0.0102226	-0.63	0.53457
c4	0.000167894	0.00020573	0.82	0.42320

Hadrurus arizonensis

Parameter	Final estimate	Standard dev.	t	Prob(t)
c0	1.24387	3.57969	0.35	0.73186
c1	-1.85832	1.82727	-1.02	0.32130
c2	0.562823	0.278068	2.02	0.05653
c3	-0.0386091	0.0159222	-2.42	0.02491
c4	0.000772574	0.00030403	2.54	0.01944

Vaejovis spinigerus

Parameter	Final estimate	Standard dev.	t	Prob(t)
c0	3.92184	3.01865	1.30	0.20733
c1	4.81083	1.9248	2.50	0.02039
c2	-0.599397	0.339771	-1.76	0.09159
c3	0.0486924	0.0211455	2.30	0.03113
c4	-0.00131585	0.000425553	-3.09	0.00532

Table 17. The statistics from the fourth order of polynomial regression on each of the scorpion species. The estimated function is $Y = C_0 + C_1 \cdot X + C_2 \cdot X^2 + C_3 \cdot X^3 + C_4 \cdot X^4$, where Y is the population size and X is the sampling time sequence. The C's are the estimated parameters.

Table 18. The estimated population sizes after the 4th order of polynomial regression.

week	<i>H. arizonensis</i>	<i>C. exilicauda</i>	<i>V. spinigerus</i>
0	0	4	6
1	0	5	9
2	0	5	12
3	0	6	14
4	0	6	16
5	1	7	18
6	2	8	19
7	4	8	21
8	5	9	23
9	7	9	25
10	8	9	27
11	9	9	30
12	9	9	32
13	9	9	35
14	9	8	38
15	9	8	40
16	8	7	42
17	7	6	43
18	6	5	44
19	5	4	43
20	4	3	41
21	3	3	38
22	3	2	32
23	3	2	24
24	3	2	14
25	2	2	5

on the numbers in this table.

Due to the infrequent ground surface activities, the relative stationary nature of the scorpions, the layout of the pitfall traps in the study sites, and the way I sample these traps, the total captured scorpions in each sampling period only represents about 20% of the true population size in the study area. This rough estimation is based on the recapture rate and the daily travelling distance of the scorpions.

b. Habitat use

Applying the same process as above to the percentage of each habitat use for each species in each sampling period, I have calculated the scorpion's habitat use index. That is also expressed in percentages. Because of the mutually exclusive nature of the two habitat properties on each habitat dimension, I only used one property from each dimension and simply call each of the habitat properties a habitat. Table 19 tabulates all the percentages of each species' habitat use.

c. Absolute population densities

The absolute population density of the scorpions on ground surface measured by the number of individuals per are (100 m²) per week are 4.3, 5.7 and 12.9 for *C. exilicauda*, *H. arizonensis* and *V. spinigerus* respectively. Because of the infrequent ground surface activities, these numbers underestimate the actual

Table 19. Percent of habitat use. v = vegetation covered habitat use; s = coarse substrate habitat use; c = small cover-rock habitat use; l = low ground level habitat use.

week	<i>C. exilicauda</i>				<i>H. arizonensis</i>				<i>V. spinigerus</i>			
	cv	cs	cc	cl	hv	hs	hc	hl	vv	vs	vc	vl
0	20	40	40	60	0	0	0	0	20	40	40	60
1	14	29	57	71	0	0	0	0	38	50	38	38
2	11	33	56	67	0	0	0	0	44	56	33	33
3	0	43	57	57	0	0	0	0	47	24	35	59
4	14	29	71	43	0	0	0	0	61	33	28	50
5	43	43	43	29	0	0	100	100	61	33	28	56
6	75	50	38	38	0	0	100	100	68	32	27	59
7	70	50	40	30	0	0	100	100	88	59	29	35
8	83	50	42	50	25	25	75	75	68	61	29	46
9	67	42	58	42	29	43	57	43	69	63	28	53
10	50	30	70	40	22	33	67	44	61	64	33	52
11	50	25	75	50	50	43	43	21	53	63	34	59
12	20	20	80	40	43	43	43	14	52	59	37	59
13	50	50	50	60	55	36	36	9	42	55	35	61
14	60	60	40	50	64	36	18	9	41	59	29	65
15	58	58	50	50	40	20	20	20	45	47	26	58
16	60	60	50	50	67	0	0	33	41	51	28	51
17	67	67	67	33	50	0	50	75	53	49	26	37
18	80	80	40	20	33	0	100	100	63	37	22	29
19	100	100	0	0	20	20	100	100	60	44	25	27
20	100	100	0	0	14	14	100	86	67	37	26	28
21	100	75	0	25	0	20	100	80	60	29	29	31
22	100	0	0	100	0	20	100	80	50	41	36	32
23	67	0	0	67	0	0	100	75	53	40	33	33
24	67	0	0	67	0	0	100	67	50	38	13	25
25	0	0	0	0	0	0	100	50	50	50	0	0

population densities of the scorpions.

C. ISOLEG ANALYSIS ON EACH SPECIES

Using the estimated population density of one species from table 18 for the x-axis, and of another species for the y-axis, I plotted in the percentages of the habitat use for the corresponding species of scorpions in table 19 to form isoleg graphs on a density state-space. Altogether, I made twenty-four such graphs. My analyses come from these graphs.

1). *C. exilicauda*

1. Vegetation cover: Individuals of *C. exilicauda* prefer the open habitat when the density of *V. spinigerus* is low (figure 16). As the density of *V. spinigerus* increases, the bark scorpions start to use both the open and the covered habitats. When *V. spinigerus* reaches its peak density and *C. exilicauda*'s density is low, *C. exilicauda* use exclusively the vegetation covered habitat. But when both *V. spinigerus* and *C. exilicauda* are at their peak densities, the bark scorpions lose their habitat preference.

At low density of *H. arizonensis*, the bark scorpions prefer the open habitat (figure 17). This preference reverses when *H. arizonensis* reach intermediate density. But when both *H. arizonensis* and *C. exilicauda* reach their highest

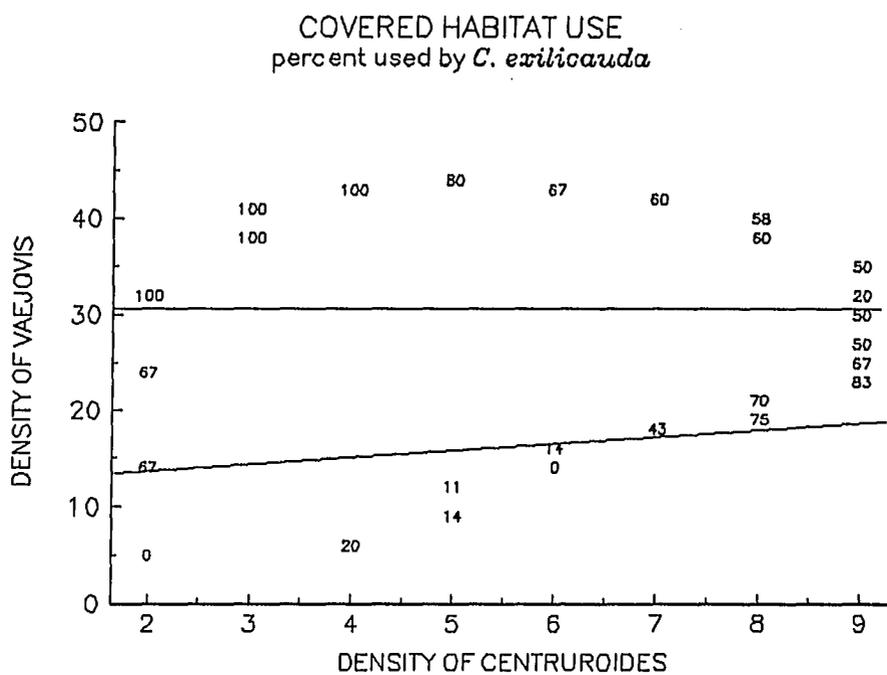


Figure 16.

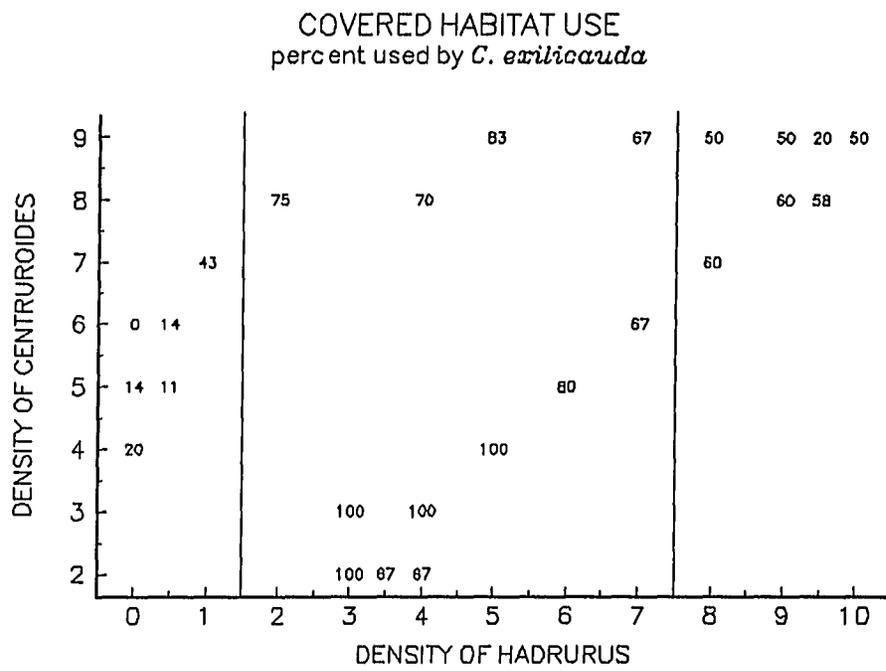


Figure 17.

densities, *C. exilicauda* uses open habitat again. I will call this seemingly weird phenomenon "reckless behavior," and discuss it in chapter 6.

Thus, the bark scorpions prefer the open habitat. But this preference depends on their own population density of their own and the densities of both *V. spinigerus* and *H. arizonensis*. When both species reached their highest densities, the bark scorpions tended to use both habitats opportunistically.

2. Substrate: The substrate use of *C. exilicauda* was primarily affected by its own density and secondarily effected by the density of *V. spinigerus*. At low density, *C. exilicauda* prefer the fine substrate habitat. This preference is lost when its own density and the density of *V. spinigerus* are intermediate. When the density of *V. spinigerus* is high and *C. exilicauda* is intermediate or high, *C. exilicauda* occurred more often in the coarse substrate (figure 18).

At low density, the bark scorpions prefer the fine substrate habitat (figure 19). At intermediate density, the bark scorpions used marginally more of the fine substrate habitats when the *H. arizonensis* were either absent or at an extremely low density; and used significantly more of the coarse substrate habitats, when the *H. arizonensis* were at intermediate or high density. At its peak density, the bark scorpions either lose their substrate preference or actually use more of the fine substrate habitats.

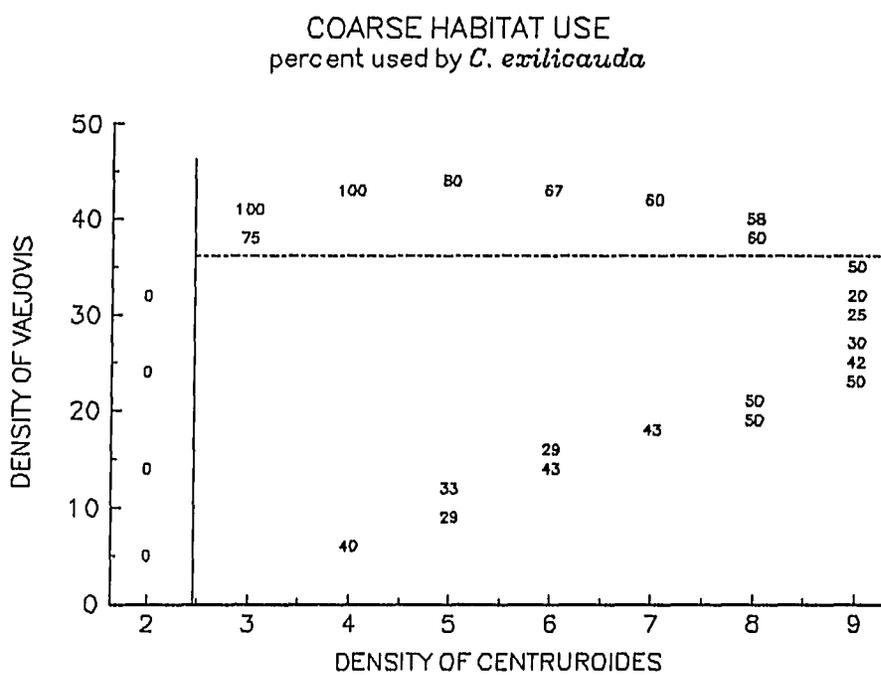


Figure 18.

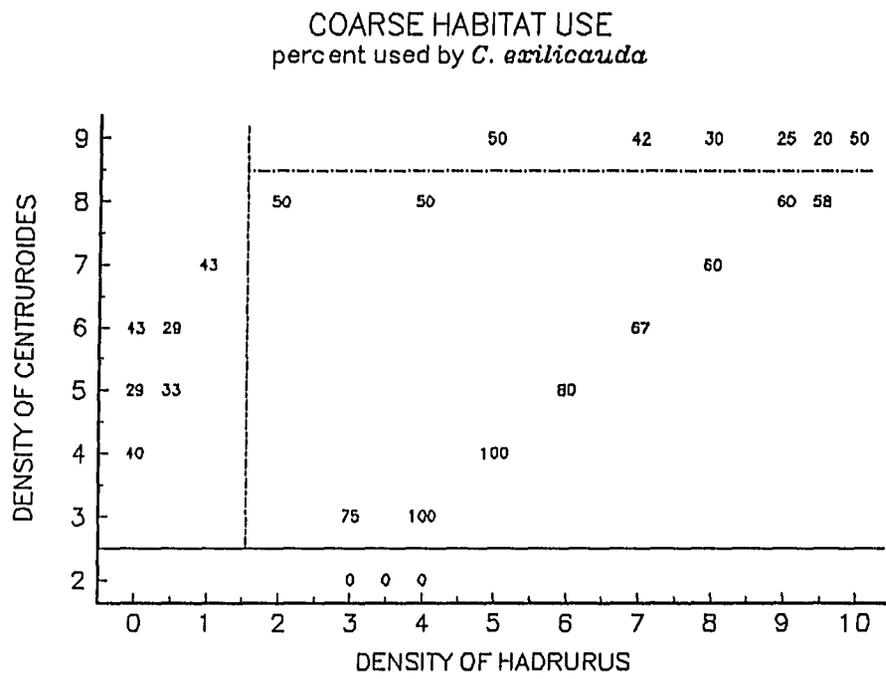


Figure 19.

3. Rock-size: The bark scorpions prefer the large cover rocks (figures 20 and 21). The densities of both *V. spinigerus* and *H. arizonensis* showed no or weak effect on *C. exilicauda* in rock size use. The size of rocks used by *C. exilicauda* is correlated only to the density of *C. exilicauda*. At low density, *C. exilicauda* prefer large rocks. This preference disappeared when more *C. exilicauda* became active on the ground surface.

4. Ground level: There is no detectable pattern in my analysis for the ground level habitat use of the bark scorpions (figures 22 and 23).

2). *H. arizonensis*

1. Vegetation cover: The vegetation use of *H. arizonensis* is only influenced by its own density (figures 24 and 25). At low density they prefer the open habitat. When their density increases to a certain level they start to accept the covered habitat.

The densities of both *C. exilicauda* and *V. spinigerus* have no influence on the *H. arizonensis*' behavior in this habitat use.

2. Substrate: *H. arizonensis* prefer to use the fine substrate all the time regardless of its own density and the density of *V. spinigerus* and of *C. exilicauda* (figures 26 and 27). The largest percentage of coarse substrate use is only 43%.

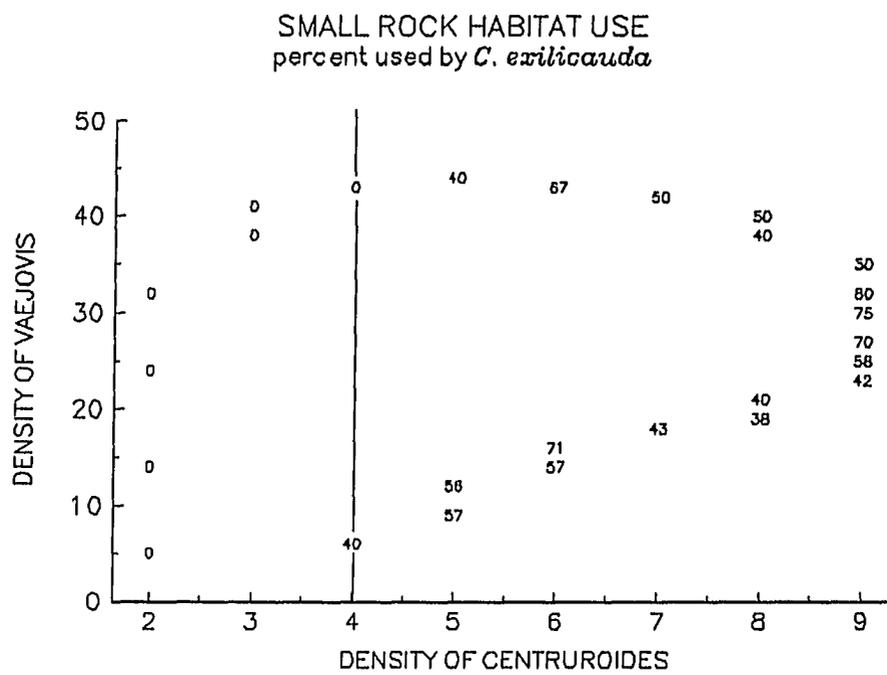


Figure 20.

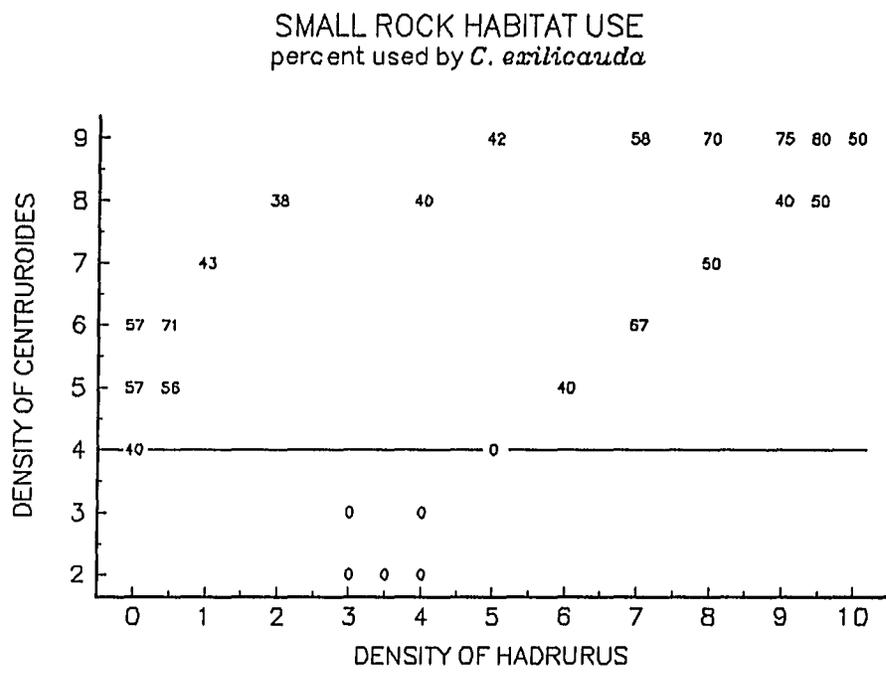


Figure 21.

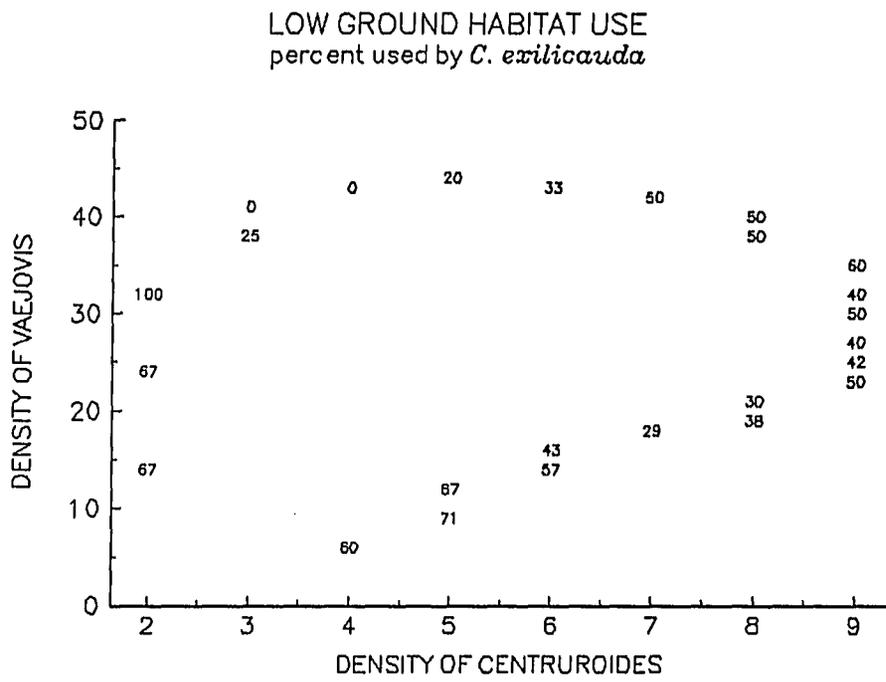


Figure 22.

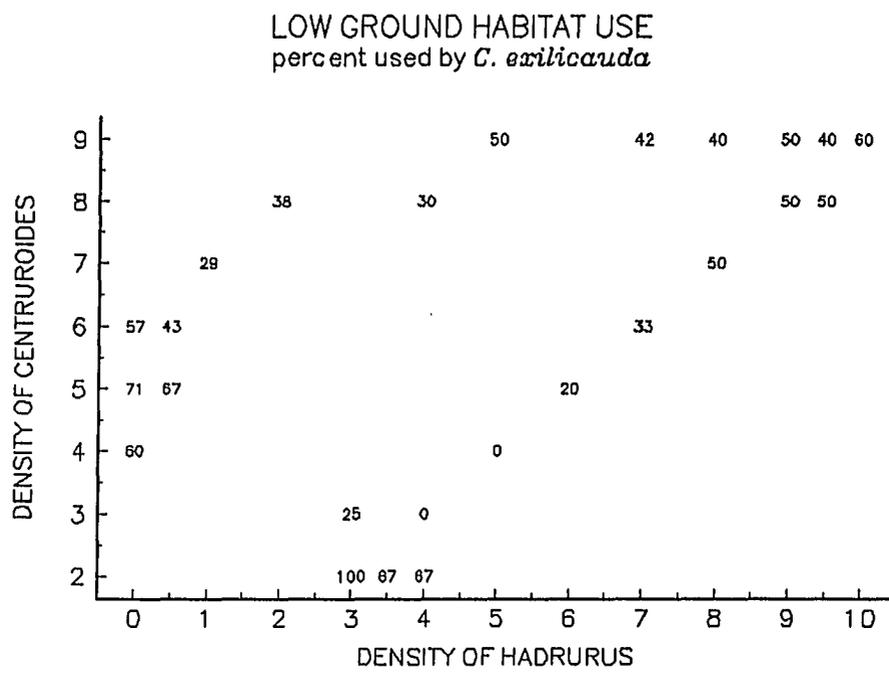


Figure 23.

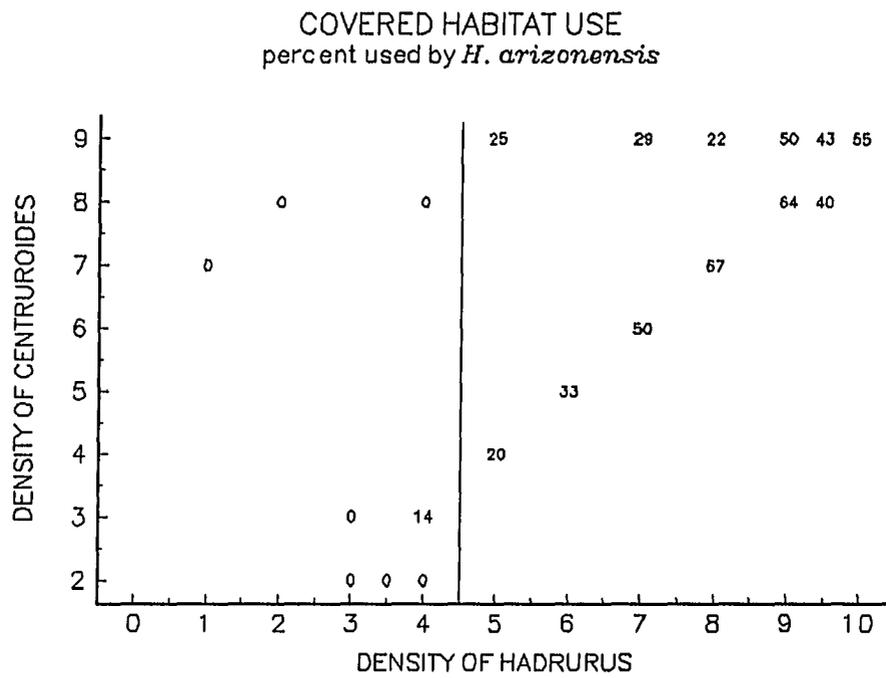


Figure 24.

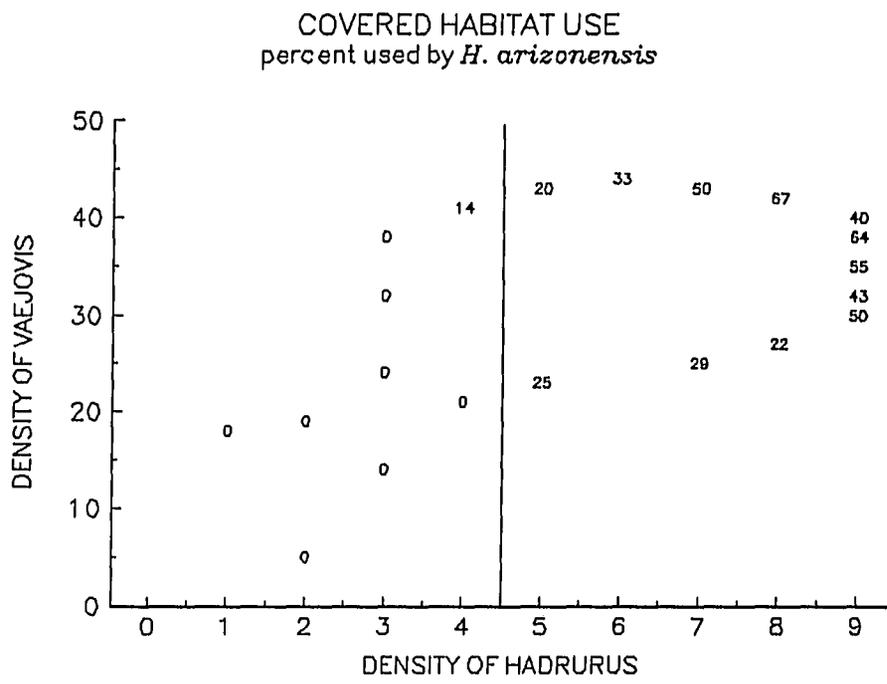


Figure 25.

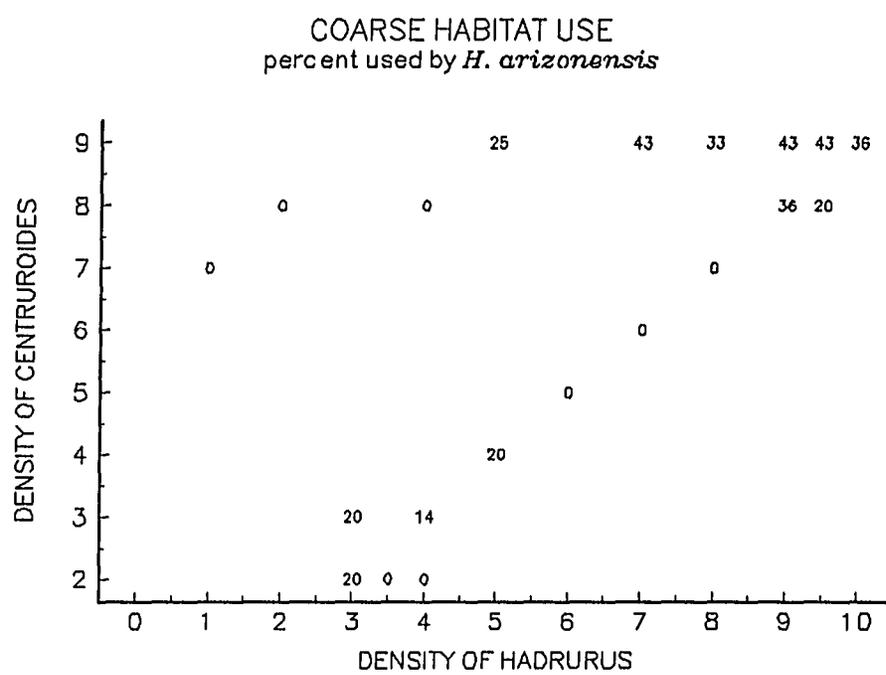


Figure 26.

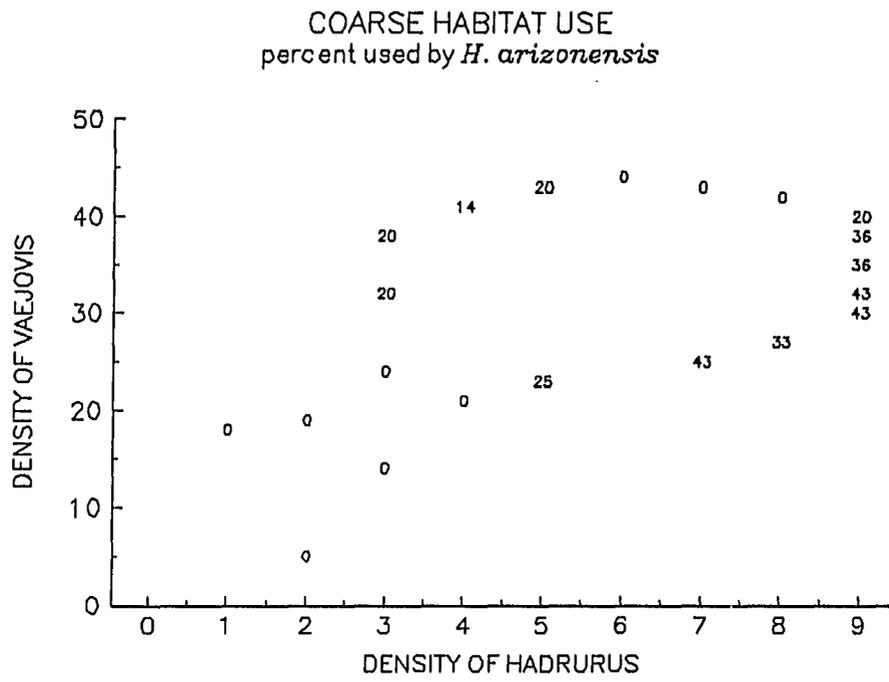


Figure 27.

But the preference certainly weakens at high *H. arizonensis* density. In fact, figure 26 suggests *C. exilicauda* plays a role.

3. Rock-size: *H. arizonensis* prefers small rocks when their density is low (figures 28 and 29). Only when their own density increases beyond a certain point, do they start to accept the large-rock habitats.

The densities of both *C. exilicauda* and *V. spinigerus* have no influence the *H. arizonensis*' use of rock size.

4. Ground level: *H. arizonensis* prefer the low ground level habitats when their density is low (figures 30 and 31). Only when their own density reaches a certain level, do they start to accept the high ground habitats.

The densities of both *C. exilicauda* and *V. spinigerus* have no effect on *H. arizonensis* in ground level habitat use.

3). *V. spinigerus*

1. Vegetation cover: *V. spinigerus* showed no preference for the open or the covered habitat, regardless of the density of *C. exilicauda* (figure 32).

However, at both high and low densities of *V. spinigerus* and *H. arizonensis*, the striped tail scorpions showed a weak preference for the open habitats (figure 33).

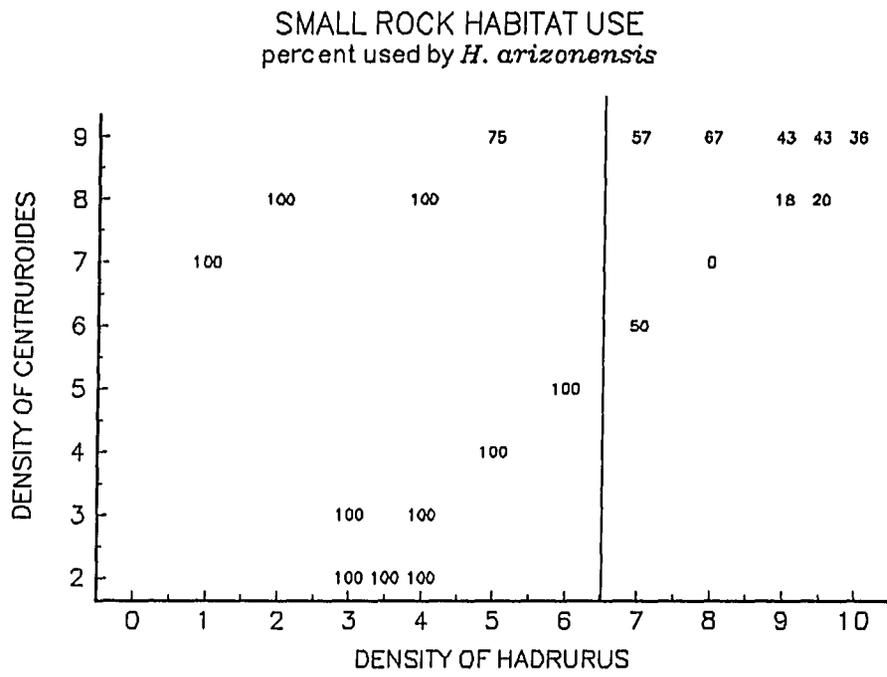


Figure 28.

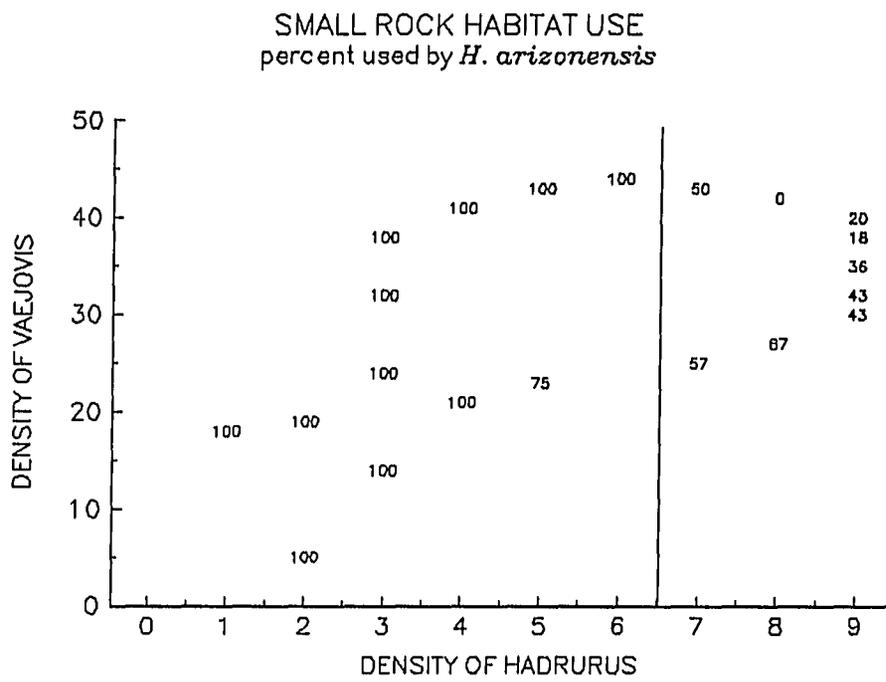


Figure 29.

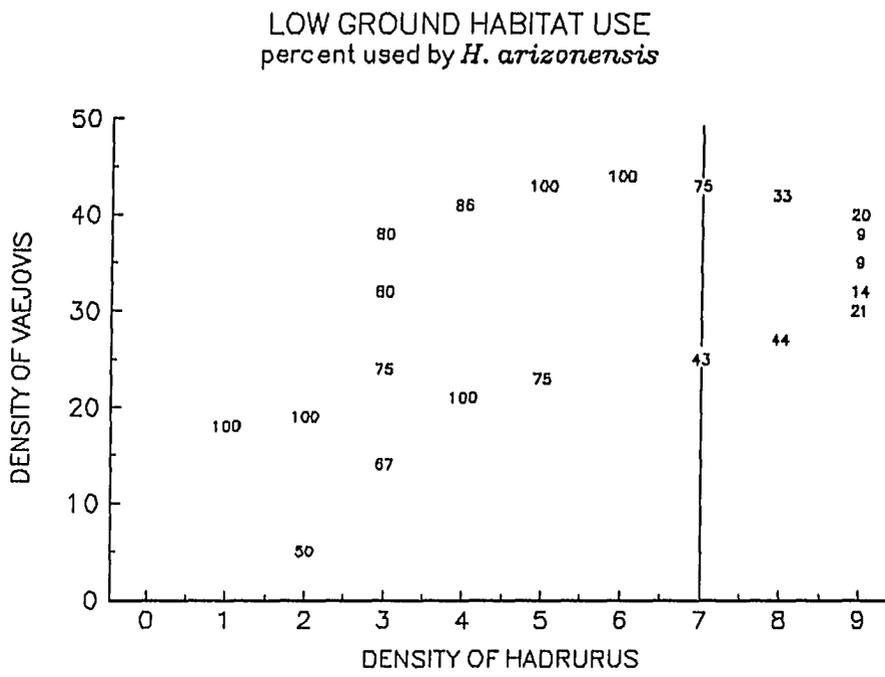


Figure 30.

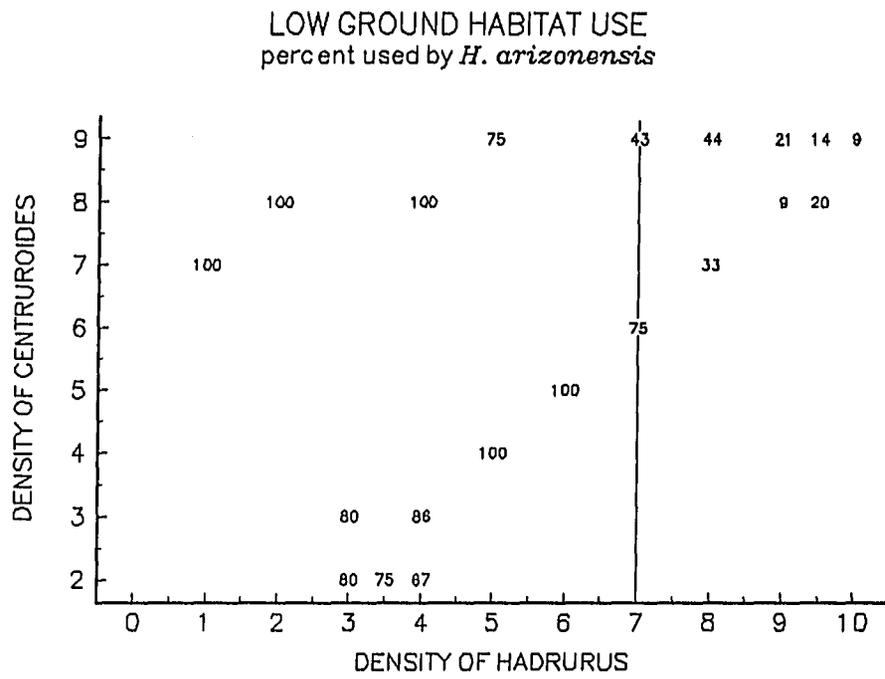


Figure 31.

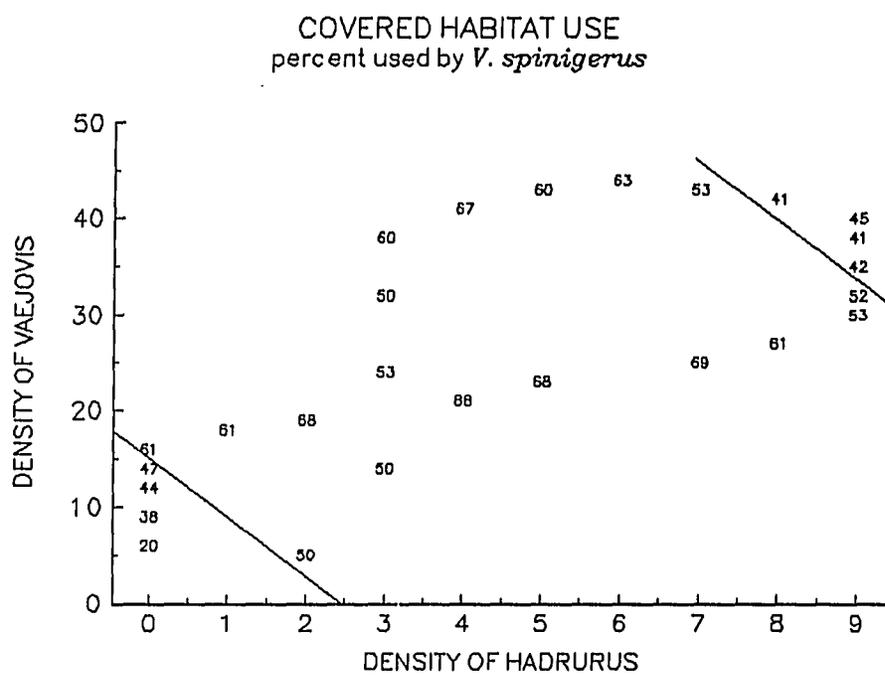


Figure 32.

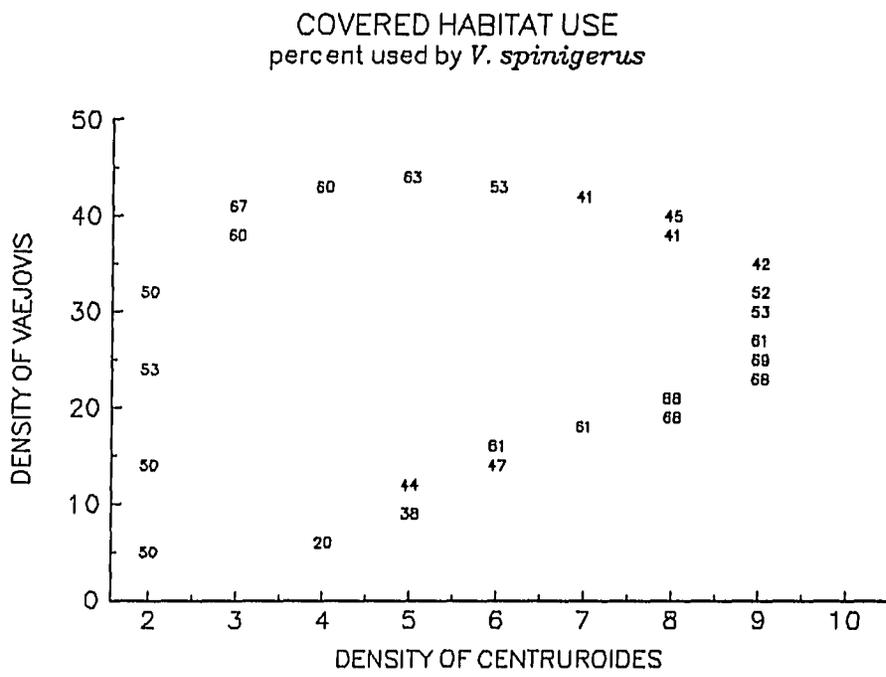


Figure 33.

2. Substrate: *V. spinigerus* showed no preference for substrate (figures 34 and 35). No patterns of habitat use could be detected in my analysis in regarding to the densities of the three species of scorpions.

3. Rock-size: *V. spinigerus* preferred large rocks consistently during my study period. At most, they would use small rocks only 37% of the time (figures 36 and 37).

4. Ground level: *V. spinigerus* showed no preference for the ground level regardless of the density of *C. exilicauda* (figure 38). But it was affected by the density of *H. arizonensis* (figure 39). At both high and low densities of *H. arizonensis*, the striped tail scorpions tend to be indifferent. But at the intermediate density of *H. arizonensis* the striped tail scorpions used more of the high ground habitats.

D. HYPOTHESES AND THEIR PREDICTIONS

Following these isoleg analysis above, I generated some hypotheses, and their associated predictions. The predictions are testable. These hypotheses and predictions outline the subject from general to specific. I will temporarily ignore the scorpions' reckless behavior in the development of the following predictions.

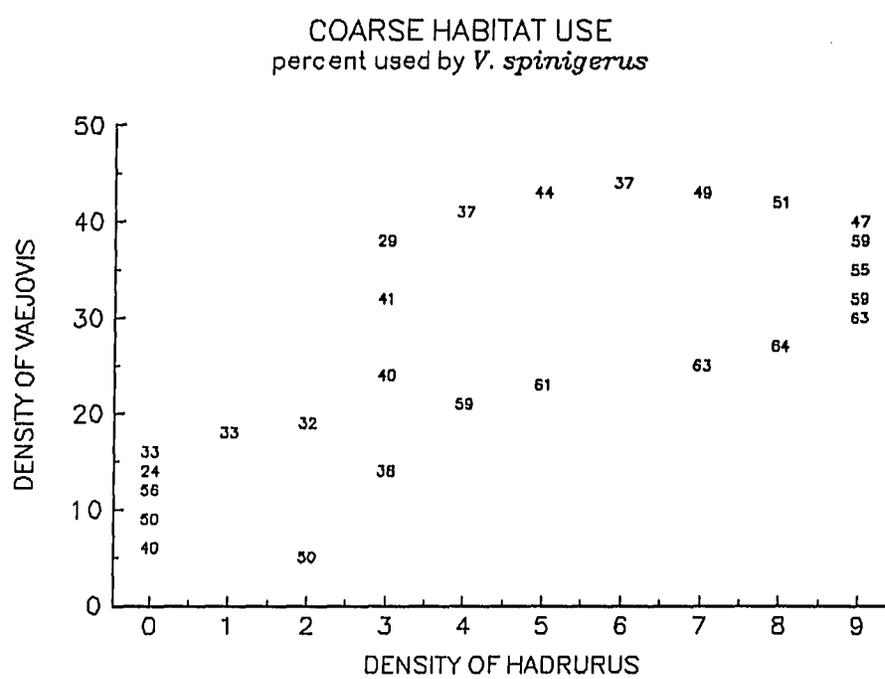


Figure 34.

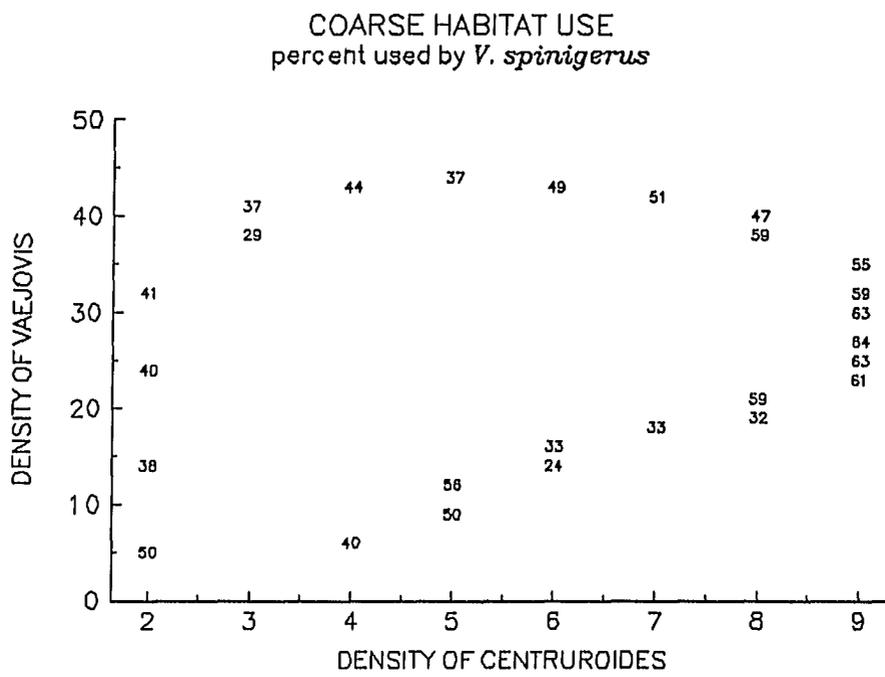


Figure 35.

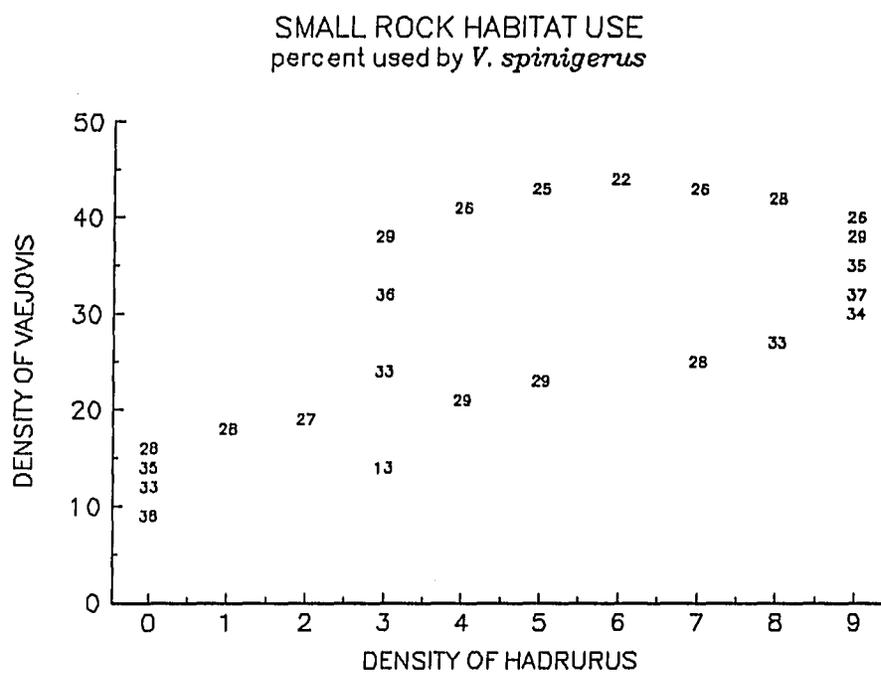


Figure 36.

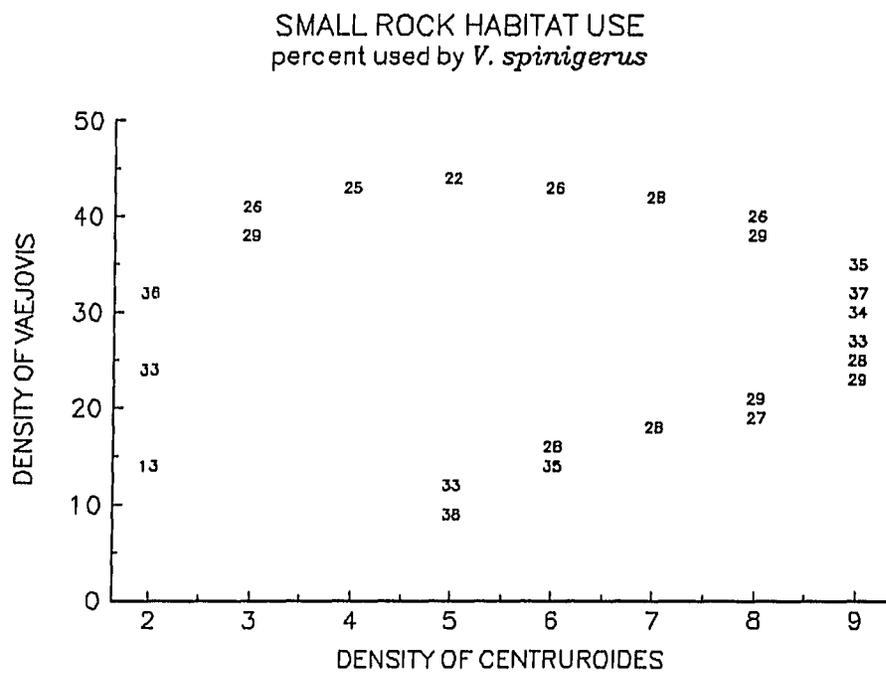


Figure 37.

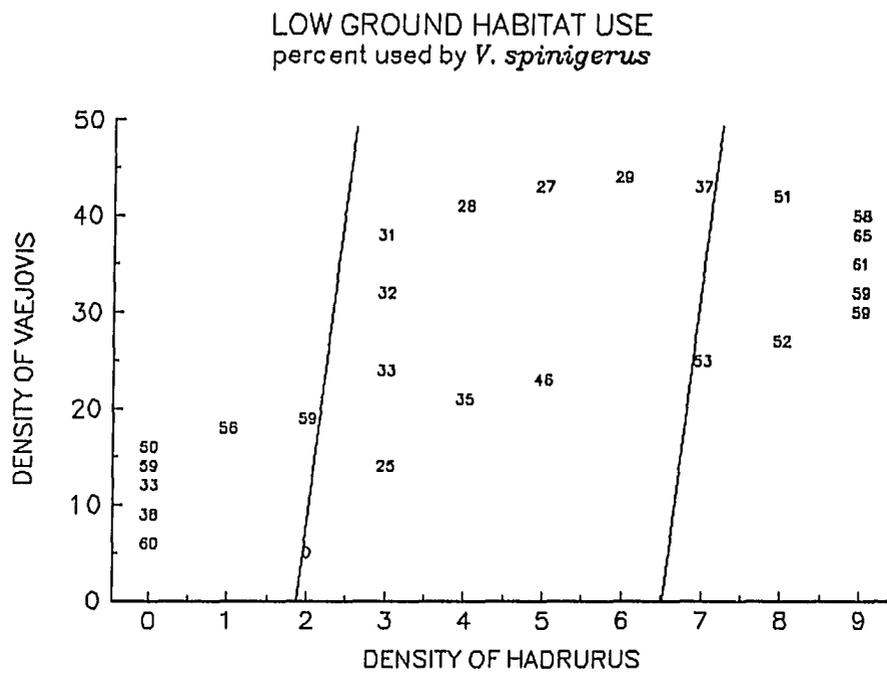


Figure 38.

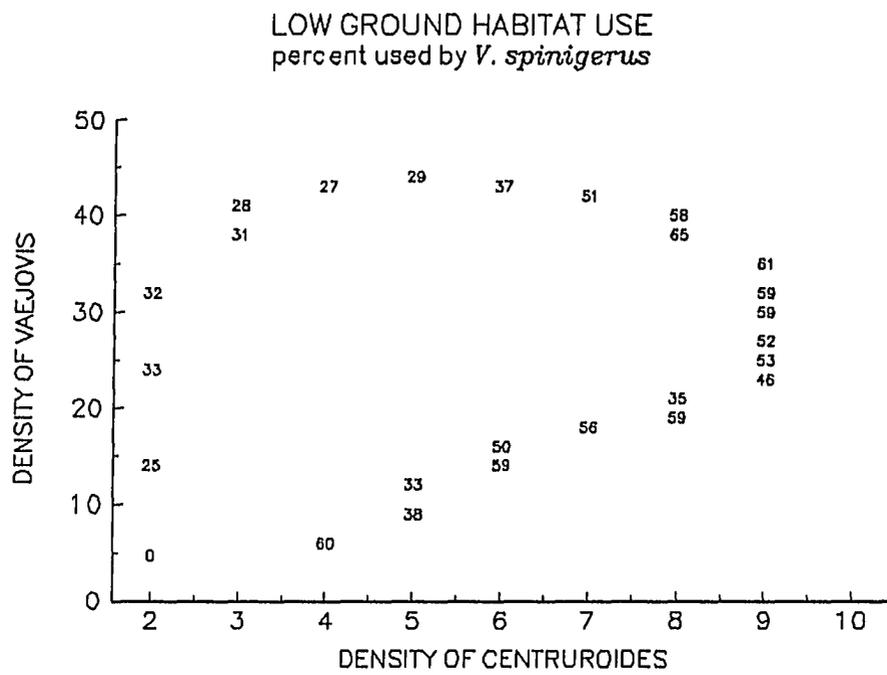


Figure 39.

But I will come back to discuss this bizarre behavior in the last chapter, community organization. Most of the predictions were tested in the same study area during the following year. I will discuss the results of these experimental tests in the next chapter.

1). *C. exilicauda*

C. exilicauda is the subordinate species of the three. Its habitat use is mostly controlled by the densities of both *H. arizonensis* and *V. spinigerus*.

I. The proportion of covered habitat used by *C. exilicauda* is directly affected by the densities of both *V. spinigerus* and *H. arizonensis*.

Predictions: 1) *C. exilicauda* will use more covered habitat when *H. arizonensis*' density is high than when it is low. 2) *C. exilicauda* will use more covered habitat when *V. spinigerus*' density is high than when it is low.

II. The substrate use of *C. exilicauda* was primarily affected by its own density, and secondarily affected by the densities of *H. arizonensis* and *V. spinigerus*.

Predictions: 1) At low density, *C. exilicauda* prefer the fine substrate habitat, regardless the densities of the other species. 2) *C. exilicauda*, at intermediate or high density, will use more coarse substrate when the density of *H. arizonensis* is high than when it is low. 3. *C. exilicauda*, at intermediate or high

density, will use more coarse substrate when the density of *V. spinigerus* is high than when it is low.

III. The amount of small rock habitat used by *C. exilicauda* depends on its own density.

Prediction: *C. exilicauda* will use more small rock habitat when its own density is high than when it's low, regardless of the densities of *H. arizonensis* and *V. spinigerus*.

IV. Individuals of *C. exilicauda* show no detectable pattern of ground level.

Prediction: The bark scorpions do not select habitat on the basis of whether they are high or low.

2). *H. arizonensis*

H. arizonensis is the dominant species of the three. Its behaviors of habitat use are mostly controlled by its own density, and not influenced by the densities of the other species of scorpions in the community.

I. The open and covered habitat use of *H. arizonensis* depends on its own density.

Prediction: *H. arizonensis* will use more covered habitats when its density is high than when it is low.

II. The substrate use of *H. arizonensis* depends neither on its own density, nor on the densities of *C. exilicauda* and *V. spinigerus*.

Prediction: *H. arizonensis* will use the fine substrate habitat consistently during their active season, regardless the density of any species of scorpions in the community.

III. The size of rocks used by *H. arizonensis* will depend on its own density only.

Prediction: *H. arizonensis* will use more large rock habitats when its density is high than when it is low.

IV. The ground level use of *H. arizonensis* depends on its own density, and is not affected by the density of *V. spinigerus* and of *C. exilicauda*.

Prediction: *H. arizonensis* will use more high ground when its own density is high.

3). *V. spinigerus*

V. spinigerus is the tolerant species of the three. Its habitat use is affected by the density and consequently the behavior of *H. arizonensis*.

I. The amount of covered habitat used by *V. spinigerus* depends on the

density of *H. arizonensis*.

Prediction: *V. spinigerus* will use more covered habitat when the density of *H. arizonensis* is high.

II. Individuals of *V. spinigerus* show no detectable preference for substrate, regardless of the density of any species of scorpions.

Prediction: The striped-tail scorpions do not select habitat along this habitat dimension.

III. The amount of small rock habitats used by *V. spinigerus* does not depend neither on scorpion density.

Prediction: *V. spinigerus* will consistently use more large rock habitats regardless its own density and the density of *C. exilicauda* and of *H. arizonensis*.

IV. The ground level use of *V. spinigerus* depends on the density of *H. arizonensis*.

Prediction: *V. spinigerus* will use more high ground habitats when the density of *H. arizonensis* is intermediate than when the density of *H. arizonensis* is low or high. The striped-tail scorpions show reckless behavior with respect to ground level use.

Most of these predictions were tested in the field in 1992. I will focus on the discussions of these tests in the next chapter. Reckless behavior will be discussed in the chapter entitled "the community structure of the desert scorpions."

CHAPTER 5. EXPERIMENTAL TEST.

A. EXPERIMENTAL DESIGN AND ASSUMPTIONS

To test the above hypotheses and their associated predictions, I went to the study sites again in 1992. The experiments started on June 28th, and lasted exactly for 19 weeks. I reused most of the pitfall traps in the field, but replaced the rusted cans. I went to the study sites once a week, and used the same sampling procedure as I did in 1991. To distinguish between the newly captured scorpions and those marked in the previous season, I put an additional mark on the rear left leg for each new capture.

Before the initiation of my experiment, I switched some rock cover within each of the study sites. But the ratio of large to small cover rocks was the same as in 1991 for each study site. I kept the other habitat types intact during the experiments.

Each scorpion species has a different preference for size of rock cover. The subordinate species, *C. exilicauda*, uses this habitat dimension in an intra-specific density dependent fashion. At low population density, they preferred the large cover rocks. The dominant species, *H. arizonensis*, has uses this habitat dimension in an intra-specific density dependent fashion as well. But they preferred the small cover rocks when their density was low. The tolerant species,

V. spinigerus, uses this habitat dimension in a density independent fashion. They use significantly more large rocks throughout the sampling seasons. And more surprising, unlike the other habitat dimensions, no species shows reckless behavior toward the rock cover dimension. I took advantage of the easy to modify character of this habitat dimension, and switched the cover rocks within each study site.

The main part of the experiment includes: adding scorpions to some sites; transferring scorpions among sites; and removing scorpions from some sites. Table 20, the experimental design, summarizes all the scorpion manipulations during the experiment. When the experiment started at the end of June, I added three individuals of *H. arizonensis* to site A; and ten individuals of *V. spinigerus* to site C. All of these 13 scorpions had been collected in the adjacent area during the previous sampling season, and kept alive in the laboratory. During the first two weeks of the experiment, I moved three *H. arizonensis* from site B into site A; four *H. arizonensis* from site C into site A. At the same period, I moved twelve adults of *V. spinigerus* from site B into site C. I did not alter the bark scorpions' densities in any site. All the added and transferred scorpions were individually marked before release. Hoping the transferred scorpions would stay within the site where they were added, I released them in the central region of each study site. After the first two weeks, I stopped adding scorpions into any of the study sites. But individuals of *H. arizonensis* from site B and site C, and individuals of *V.*

Table 20. The experimental design, and scorpion transformation. C is for *C. exilicauda*; H is for *H. arizonensis*; and V is for *V. spinigerus*.

study site	manipulation	results
a	+H	C H+3b+4c+3 V
b	-H, -V	C H-3 V-12
c	-H,+V	C H-4 V+12b+10

spinigerus from site B were continuously removed from these sites throughout the experiment.

B. SUCCESS OF THE EXPERIMENT

I spent nineteen early Sunday mornings in the field checking the pitfall traps. During this period, 47 *C. exilicauda*, 43 *H. arizonensis* and 224 *V. spinigerus* fell into the pitfalls. Among these, 4 *C. exilicauda*, 7 *H. arizonensis* and 31 *V. spinigerus* had been marked during 1991. Thus, the recapture rate between the two sampling seasons was 9.76% for *C. exilicauda*, 29.17% for *H. arizonensis*, and 14.22% for *V. spinigerus*. These percentages give a general indication about survivorship of scorpion populations.

Table 21 summarizes the total scorpions trapped during the experiment in 1992. The data include those individuals transferred and added to each corresponding study site. For those scorpions removed from site B and site C, their only trapping record is also included in the table.

To test the hypothesis that the abundance of each species is the same across the study sites, I did three Chi-square tests. The Chi-square value is 4.383 for *C. exilicauda*, 9.814 for *H. arizonensis* and 6.277 for *V. spinigerus*. At a 5% significance level with two degrees of freedom, the statistics are significant for *H. arizonensis* and *V. spinigerus*. This shows the success of the transplanting

Table 21. The trapped scorpions in each study site during the experiment in 1992.

study site	<i>C. exilicauda</i>	<i>H. arizonensis</i>	<i>V. spinigerus</i>	sum
A	20	24	69	113
B	9	10	63	82
C	18	9	92	119
total	47	43	224	314

experiment. The same tests conducted on the data collected in 1991 had shown insignificant results.

C. HYPOTHESIS TESTING

Because of the limits of the experimental design, I cannot test all of the predictions. But the majority of them were tested. Whenever a test does not properly apply, I usually try a simple method.

For clarity, I will repeat here the hypotheses and predictions. The test, of course, will follow each of the predictions. Most of the tests conducted are pairwise comparisons between the study sites. Thus, two-by-two or three-by-two contingency-table tests will suffice the purpose. But I am also fully aware the fact that violations of some statistic rules are inevitable. The violations mainly arrive from my small sample size. For instance, some tests will violate the rule of thumb that the expected value should be equal or greater than five in Chi-square testing. Whenever this occurs, I will try an alternate test if it is possible.

I have tabulated in table 22 the total captures and the absolute frequencies of habitat use of the scorpions. Further, I extracted data from table 22 to construct twelve tables, table 23 to 34. All the following tests are based on one of these tables.

Table 22. The absolute frequency of habitat used by the scorpions.

	<i>C. exilicauda</i>	<i>H. arizonensis</i>	<i>V. spinigerus</i>
site A			
total captures	20	24	69
covered habitat	12	4	47
coarse habitat	10	6	40
small rock habitat	10	11	20
low ground habitat	11	13	33
site B			
total captures	9	10	63
covered habitat	2	1	14
coarse habitat	4	3	28
small rock habitat	1	9	20
low ground habitat	2	0	14
site C			
total captures	18	9	92
covered habitat	13	1	26
coarse habitat	11	3	47
small rock habitat	6	7	36
low ground habitat	7	2	25

Table 23. The covered and open habitat use of *C. exilicauda*.

study site	covered habitat	open habitat
A	12	8
B	2	7
C	13	5

Table 24. The coarse and fine substrate use of *C. exilicauda*.

study site	coarse substrate	fine substrate
A	10	10
B	4	5
C	11	7

Table 25. The small and large rock habitat use of *C. exilicauda*.

study site	small rock	large rock
A	10	10
B	1	8
C	6	12

Table 26. The high and low ground habitat use of *C. exilicauda*.

study site	low ground	high ground
A	11	9
B	2	7
C	7	11

Table 27. The covered and open habitat use of *H. arizonensis*.

study site	covered habitat	open habitat
A	9	15
B	1	9
C	1	8

Table 28. The coarse and fine substrate use of *H. arizonensis*.

study site	coarse substrate	fine substrate
A	6	18
B	3	7
C	3	6

Table 29. The small and large rock habitat use of *H. arizonensis*.

study site	small rock	large rock
A	11	13
B	9	1
C	7	2

Table 30. The high and low ground habitat use of *H. arizonensis*.

study site	low ground	high ground
A	13	11
B	0	10
C	2	7

Table 31. The covered and open habitat use of *V. spinigerus*.

study site	covered habitat	open habitat
A	47	22
B	14	49
C	26	66

Table 32. The coarse and fine substrate use of *V. spinigerus*.

study site	coarse substrate	fine substrate
A	40	29
B	28	35
C	47	45

Table 33. The small and large rock habitat use of *V. spinigerus*.

study site	small rock	large rock
A	20	49
B	20	43
C	36	56

Table 34. The high and low ground habitat use of *V. spinigerus*.

study site	low ground	high ground
A	33	36
B	14	49
C	25	67

1). *C. exilicauda*

C. exilicauda is the subordinate species of the three. Its habitat use is mostly controlled by the densities of both *H. arizonensis* and *V. spinigerus*.

Hypothesis: I. The proportion of covered habitat used by *C. exilicauda* is directly affected by the densities of both *V. spinigerus* and *H. arizonensis*.

Prediction 1): *C. exilicauda* will use more covered habitat when *H. arizonensis*' density is high than when it is low.

Test: Because of the addition of *H. arizonensis* to study site A, and the removal of the same species from study site B and C, it is appropriate to test the behavior of *C. exilicauda* in site A against those in site B and C together. But as many individuals of *V. spinigerus* were added into site C, the behavior of *C. exilicauda* in this site could be heavily influenced by *V. spinigerus* instead of *H. arizonensis*. So I eliminated the data from site C in table 23 for this test.

To test if the *C. exilicauda* from site A and site B use the same proportion of the covered and open habitats, I did a Chi-square test. At 5% significant level with one degree of freedom, the result, $X^2=3.548$, is less than 3.841. Thus, the individuals of *C. exilicauda* from site A and site B use the same proportion of the covered or open habitats. The density of *H. arizonensis* does not significantly influence the behavior of *C. exilicauda* toward this habitat dimension. The prediction fails.

Prediction 2): *C. exilicauda* will use more covered habitat when *V.*

spinigerus' density is high than when it is low.

Test: I have added individuals of *V. spinigerus* into site C and have removed some from site B. Thus, significantly more *V. spinigerus* exist in site C than in site B. Because the density of *V. spinigerus* in site A was unchanged, I only use the data from site B and site C in table 4-4 to test this prediction.

To test whether the *C. exilicauda* from these two sites use the same proportion of the covered and open habitats, I did a Chi-square test. At 5% significant level with one degree of freedom, the result, $X^2=6.075$, is greater than 3.841. Thus, I conclude that individuals of *C. exilicauda* in site B used the covered or open habitats differently as in site C. In other words, the density of *V. spinigerus* does significantly influence the behavior of *C. exilicauda* on this habitat dimension.

Hypothesis: II. The substrate use of *C. exilicauda* was primarily affected by its own density, and secondarily affected by the density of *H. arizonensis* and of *V. spinigerus*.

Prediction 1): At low density, *C. exilicauda* prefers the fine substrate habitat, regardless of the densities of the other species.

Test: I did not manipulate the densities of *C. exilicauda*, so I have not tested this prediction.

Prediction 2): *C. exilicauda*, at intermediate or high density, will use more

coarse substrate when the density of *H. arizonensis* is high than when it is low.

Test: Assuming that the density of *C. exilicauda* in all sites are high, I used the data from site A and site B in table 24 to test this prediction.

To test whether the *C. exilicauda* from these two sites use the same proportion of the coarse and fine substrate habitats, I did a Chi-square test. At 5% significant level with one degree of freedom, the result, $X^2=0.077$, is less than 3.841. Thus, I conclude that individuals of *C. exilicauda* from site A and site B use the coarse or fine substrate habitats in the same proportion. In other words, the density of *H. arizonensis* does not significantly influence the behavior of *C. exilicauda* on this habitat dimension.

Prediction 3): *C. exilicauda*, at intermediate or high density, will use more coarse substrate when the density of *V. spinigerus* is high than when it is low.

Test: Site C has significantly more *V. spinigerus* than in site B. Thus, I used the data of site B and site C in table 24 to test this prediction.

To test whether the *C. exilicauda* from these two sites use the same proportion of the coarse and fine substrate habitats, I did a Chi-square test. At 5% significant level with one degree of freedom, the result, $X^2=0.675$, is less than 3.841. Thus, I conclude that individuals of *C. exilicauda* from site B and site C use the coarse or fine substrate habitats in the same proportion. In other words, the density of *V. spinigerus* does not significantly influence the behavior of *C. exilicauda* on this habitat dimension.

Hypothesis: III. The amount of small rock habitat used by *C. exilicauda* depends on its own density, and completely independent with the density of *H. arizonensis* and of *V. spinigerus*.

Prediction: *C. exilicauda* will use more small rock habitat when its own density is high than when it's low, regardless of the densities of *H. arizonensis* and *V. spinigerus*.

Test: I did not manipulate the densities of *C. exilicauda*, so I cannot test this prediction. But I can use the data in table 25 plus the bark scorpion's density in each site to simply ask: 1) if this species uses the concerned habitat in similar proportion in all the study sites; and 2) if there is a simply correlation between bark scorpion's density and the percentage of small rock habitat use.

First, to test whether *C. exilicauda*' behavior in using this habitat differ from each study site, I conducted a chi-square test. At 5% significant level with two degree of freedom, the result, $X^2=4.168$, is less than 5.991. Thus, I conclude that individuals of *C. exilicauda* did not differ from site to site in using the small and large rock habitats. In other words, the density of *V. spinigerus* and of *H. arizonensis* does not significantly influence the behavior of *C. exilicauda* on this habitat dimension.

Further, I did a simple linear regression on *C. exilicauda*'s densities (They are 20, 9, and 18 for site A, B and C respectively) against the percentage of small rock use in the corresponding site (They are 50%, 12.5% and 33.3% respectively).

The result, $R^2=0.919$, shows a positive correlation between *C. exilicauda*'s density and the amount small rock habitat used.

Hypothesis: IV. Individuals of *C. exilicauda* show no detectable pattern of ground level use.

Prediction: The bark scorpions do not select habitats on the basis of whether they are high or low.

Test: To test whether the *C. exilicauda* used the same proportion of low and high ground level habitats, I used the data in table 26 to conducted a three-by-two-contingency table test.

At 5% significant level with two degree of freedom, the result, $X^2=2.888$, is less than 5.991. Thus, I conclude that individuals of *C. exilicauda* did not differ in using the high and low ground level habitats.

2). *H. arizonensis*

H. arizonensis is the dominant species of the three. Its habitat use is mostly controlled by its own density, and not influenced by the densities of the other species of scorpions.

Hypothesis: I. The open and covered habitat use of *H. arizonensis* depends on its own density, and not related to the density of *C. exilicauda* and of *V. spinigerus*.

Prediction: *H. arizonensis* will use more covered habitats when its density is high than when it is low.

Test: Study site A has a significantly higher density of *H. arizonensis* than either site B or site C. To increase the sample size, I combined the data from site B and site C in table 27. Using the combined data and these from site A, I constructed a two-by-two-contingency table.

To test whether the *H. arizonensis* from these sites using the same proportion of the covered and open habitats, I did a Chi-square test. At 5% significant level with one degree of freedom, the result, $X^2=4.053$, is greater than 3.841. Thus, individuals of *H. arizonensis* do use a larger proportion of covered habitats when they become more abundant. In other words, the density of *H. arizonensis* does significantly influence their behavior of on this habitat dimension.

Hypothesis: II. The substrate use of *H. arizonensis* depends neither on its own density, nor on the density of *C. exilicauda* and of *V. spinigerus*.

Prediction: *H. arizonensis* will consistently use a large proportion of the fine substrate habitat in all the study sites, regardless the density of any species of scorpions in the community.

Test: The total fine substrate habitat uses are 75%, 70% and 67% in study site A, B and C respectively. These percentages indicate the fact that *H. arizonensis* prefer the fine substrate habitat in a density independent manner.

To test if the giant hairy scorpions used the substrate habitat differently from site to site, I used the data from table 28 to conduct a Chi-square test. At 5% significant level with two degree of freedom, the result, $X^2=0.254$, is less than 5.991. Thus, individuals of *H. arizonensis* used more proportion of the fine substrate through all the study sites.

Hypothesis: III. The size of rocks used by *H. arizonensis* will depend on its own density only.

Prediction: *H. arizonensis* will use more large rock habitats when its density is high than when it is low.

Test: Study site A has a significantly higher density of *H. arizonensis* than does either site B or site C. To test the above prediction, I combined the data from site B and site C in table 29. Using the combined data and these from site A, I constructed a two-by-two table.

To test whether the *H. arizonensis* from these sites using the same proportion of the small rock and large rock habitats, I did a Chi-square test. At 5% significant level with one degree of freedom, the result, $X^2=6.685$, is greater than 3.841. Thus, individuals of *H. arizonensis* do use a larger proportion of the large rock habitats when they become more abundant. In other words, the density of *H. arizonensis* does significantly influence their own behavior on this habitat dimension.

Hypothesis: IV. The ground level use of *H. arizonensis* depends on its own density, and is not affected by the density of *V. spinigerus* and of *C. exilicauda*.

Prediction: *H. arizonensis* will use more high ground when its own density is high than when it is low.

Test: Study site A has a significantly higher density of *H. arizonensis* than either site B or site C. To test the above prediction, I once again combined the data from site B and site C in table 30. Using the combined data and these from site A, I constructed a two-by-two table.

To test whether the *H. arizonensis* from these sites using the same proportion of the low ground level and high ground level habitats, I did a Chi-square test. At 5% significant level with one degree of freedom, the result, $X^2=2.694$, is less than 3.841. Thus, individuals of *H. arizonensis* do not use more high ground level habitats when they become more abundant. In other words, the density of *H. arizonensis* does not significantly influence their own behavior on this habitat dimension.

3). *V. spinigerus*

V. spinigerus is the tolerant species of the three. Its habitat use is affected by the density and consequently by the behavior of *H. arizonensis*.

Hypothesis: I. The amount of covered habitat used by *V. spinigerus* depends on the density of *H. arizonensis*.

Prediction: *V. spinigerus* will use more covered habitat when the density of *H. arizonensis* is high.

Test: Study site A has a significantly higher density of *H. arizonensis* than either site B or site C. To test the above prediction, I use the combined data from site B and site C plus these from site A in table 31 to construct a two-by-two table.

To test whether the *V. spinigerus* from these sites using the same proportion of the covered and the open habitats, I did a Chi-square test. At 5% significant level with one degree of freedom, the result, $X^2=35.980$, is far greater than 3.841. Thus, individuals of *V. spinigerus* do use more covered habitat when *H. arizonensis* become more abundant. In other words, the density of *H. arizonensis* does significantly influence the behavior of *V. spinigerus* on this habitat dimension.

Hypothesis: II. Individuals of *V. spinigerus* show no detectable preference for substrate, regardless of the density of any species of scorpions.

Prediction: The striped-tail scorpions do not select habitat along this habitat dimension.

Test: To test if the *V. spinigerus* used the substrate habitats in different proportion from site to site, I used the data from table 32 to conduct a three-by-two-contingency table test.

At a 5% significance level with two degree of freedom, the result,

$X^2=2.416$, is less than 5.991. Thus, individuals of *V. spinigerus* do not differentiate the coarse or the fine substrate habitats from site to site. In other words, *V. spinigerus* do not treat substrate as a critical habitat dimension.

Hypothesis: III. The amount of small rock used by *V. spinigerus* does not depend on scorpion density.

Prediction: *V. spinigerus* will consistently use more large rock habitats regardless its own density and the density of *C. exilicauda* and of *H. arizonensis*.

Test: Table 33 shows the data of rock-size habitat used by *V. spinigerus*. The total large-rock-habitat use are 71%, 68% and 61% in study site A, B and C respectively. These percentages indicate the fact that *V. spinigerus* prefer the large rock habitat in a density independent manner.

To test if the *V. spinigerus* consistently use a large proportion of large rock habitat in all the sites, I conducted a Chi-square test on table 33. At 5% significant level with two degree of freedom, the result, $X^2=1.996$, is less than 5.991. This confirms the prediction.

Hypothesis: IV. *V. spinigerus* had no preference on either the low or the high ground level habitats, but their use on this habitat dimension depends on, at some point, the density of *H. arizonensis*.

Prediction: *V. spinigerus* will use more high ground habitats when *H.*

arizonensis increases its density to an intermediate level. Below or above this density level, *V. spinigerus* will use the two habitat types equally.

Test: The data in table 34 shows that 52% of *V. spinigerus* in site A, 78% in site B, and 73% in site C use high ground level habitat. Assuming that *H. arizonensis* has intermediate density in site B and C, and high density in site A, I combined the data from site B and site C. Using the combined data and these from site A, I constructed a two-by-two table.

At a 5% significance level with one degree of freedom, the result, $X^2=11.245$, is greater than 3.841. Thus, *V. spinigerus* used the ground level habitat in different proportion across the study site. This confirms the main part of the prediction.

D. RESULTS

Table 35 summarizes the results of the experimental testings. Most of these tests support the predictions. Here, I will list the general results that come directly from the testings.

1). Habitat use of *C. exilicauda*

Unlike the prediction stated, the density of *H. arizonensis* does not influence the behavior of *C. exilicauda* on the open and covered habitats significantly. But, the density of *V. spinigerus* does significantly influence the

Table 35. Summary of the experimental results.

Habitat Dimension	<i>C. exilicauda</i>	<i>H. arizonensis</i>	<i>V. spinigerus</i>
vegetation	Habitat use depends on: 1. <i>H. arizonensis</i> NO 2. <i>V. spinigerus</i> YES	Habitat use depends on: 1. <i>H. arizonensis</i> YES	Habitat use depends on: 1. <i>H. arizonensis</i> YES
substrate	Habitat use depends on: 1. <i>C. exilicauda</i> YES 2. <i>H. arizonensis</i> NO 3. <i>V. spinigerus</i> NO	Habitat use depends on neither species' density. YES	No preference for this habitat. YES
rock-size	Habitat use depends on: 1. <i>C. exilicauda</i> YES	Habitat use depends on: 1. <i>H. arizonensis</i> YES	Habitat use depends on neither species' density. YES
ground-level	No preference for this habitat. YES	Habitat use depend on: 1. <i>H. arizonensis</i> YES	Habitat use depend on: 1. <i>H. arizonensis</i> NO

behavior of *C. exilicauda* on this habitat dimension.

At its low density (≤ 2 individuals trapped per study site), *C. exilicauda* prefers the fine substrate habitat, regardless the densities of the other species. But as the density of bark scorpions increases, unlike the predicted, the density of *H. arizonensis* and of *V. spinigerus* does not significantly influence the behavior of *C. exilicauda* on this habitat dimension.

As predicted, the density of *V. spinigerus* and of *H. arizonensis* does not significantly influence the behavior of *C. exilicauda* on the large and small rock habitat dimension. Instead, the amount small rock habitat used by the bark scorpions depends only on their own density.

C. exilicauda, as predicted, did not differ on the high and low ground level habitats regardless the density of the giant hairy and of the striped-tail scorpions.

2). Habitat use of *H. arizonensis*

As predicted, individuals of *H. arizonensis* did use a large proportion of the covered habitat when their density is significantly high. And the other species of scorpions had no influence on the giant hairy scorpions on this habitat dimension.

Regardless the density differences in the study sites, *H. arizonensis* always prefer the fine substrate habitat. Such preference is density independent.

The size of rocks used by *H. arizonensis*, as predicted, depended on its own density only, regardless the densities of the other species of scorpions.

Unlike the predicted, the density of *H. arizonensis* does not influence their own behavior on the low and high ground level habitats.

3). Habitat use of *V. spinigerus*

As predicted, the density of *H. arizonensis* does significantly influence the behavior of *V. spinigerus* on the open and covered habitat dimension.

V. spinigerus did not treat substrate as a critical habitat dimension. As shown in the test, the striped-tail scorpions did not differentiate on this habitat dimension regardless the density of other scorpions.

As predicted, *V. spinigerus* did consistently use more large rock habitat in all study sites. And they shown such behavior in a density independent fashion. This includes both inter-specific and intra-specific.

As predicted again, *V. spinigerus* had no preference on either the low and the high ground level habitats in all the study sites. But, as shown in the test, their behavior on this habitat dimension depends on the density of *H. arizonensis*.

E. DISCUSSION

All of the techniques I have applied in the tests above are simple and straight forward. Most of them have been conducted based on comparisons between the study sites. Three consequences made such comparisons applicable.

1) The densities of both h. and of v. differed significantly from site to site; 2) The densities of c. in the study sites did not differ significantly from one another; 3) No significance on the scorpions' density among the study sites could be detected in the previous season. In other words, the scorpions were equally distributed among the study sites before I did the experiment.

Small sample size hampers some of the tests. As pointed out early, I had inevitably to violate some statistical rules during the application of X^2 tests. The major cause of this is attributable to my small sample size. But the majority of the tests are quite reliable.

The successful testings have shown the power and robustness of the isoleg analysis. Among the fifteen tested predictions, eleven of them have resulted positively. That is 73%. And the rest have resulted negatively. Yet, most the rejected predictions derived originally from very weak and vague foundations either biologically or statistically.

The scorpions' community organization has emerged. For instance, the giant hairy scorpions' behavior only count on their own density, and the striped tail scorpions' behavior only count on the density of the giant hairys. However, the bark scorpions' behavior depend not only on their own density but also on the density of the striped tail scorpions. And more surprisingly, the bark scorpions did not select their habitats in accordance to the density of the giant hairys. All these behavioral patterns support the hypotheses derived directly from the isoleg

analysis.

In the next chapter, I will focus my discussion on the community structure of the desert scorpions.

CHAPTER 6. COMMUNITY STRUCTURE OF THE DESERT SCORPIONS.

A. INTRODUCTION

The role that scorpions play in their community is poorly known. Most researches had concentrated on community composition. In this direction two general patterns of scorpion-community composition. These patterns could occur in either scorpion-rich or scorpion-poor community (Polis, 1990). Heavily skewed species distribution characterizes the first pattern. Lourenço (1975) in Brazil and Williams (1980) in North America had noticed this pattern in their studied scorpion communities. Evenly distributed species characterizes the second pattern. Gertsch and Allred (1965) in Nevada, and Williams (1971, 1980) in Baja California have noticed this pattern exhibited by the local scorpions. Usually these distribution patterns variate wildly, sometimes even within one species in a narrow geographical range. For instance, Williams (1980) has found that *C. exilicauda* composed from less than 1 percent to 92 percent of all scorpions at 35 sites in Baja California. Such composition variation also exists in the desert sand scorpion, *Paruroctonus mesaensis* (Hadley and Williams, 1968; Fox, 1975; Polis, 1979). The mechanism associated with these composition patterns is unknown.

Habitat selection probably sustains the key mechanism in answering the composition questions. One pioneer study conducted by Stanley Williams (1970)

at Phoenix South Mountain enriched such possibility. Worked with three species of desert scorpions, Williams concluded that habitat specialization and prey size choice were the most important factors in shaping scorpion communities. Prey size, however, correlated positively with the size of scorpions (Stahnke, 1966; Francke, 1979). So, the paramount determinants of species composition and community structure are most likely to be habitat selection and body size of the scorpions.

In this chapter, I will discuss the community organization of the scorpions in the West of Tucson Mountain area. I will emphasize the discussions in terms of habitat selection and body size differences. Special attention will focus on the following questions. What role does habitat selection play in determine the scorpions' relative density? How do the population densities influence the scorpions' behavior in habitat selection? How do these behaviors facilitate the coexistence of the scorpions? And finally, I will end the discussion by comparing community organizations of my system with the others.

B. POPULATION DENSITY AND HABITAT USE

Population density and habitat selection depend on each other. In a large sense, this rule holds universally. But treated specifically, tremendous variation occurs. This is especially true when scorpions are compared across different

habitats. For instance, the bark scorpions switched their substrate habitat use when their captures exceeded two in a study site. But they started to accept the less preferred small-rock habitat only when their captures exceeded four in a study site. This instance and many others shown the evidence that population density has different meaning to scorpions when they face different habitat dimensions. In other words, it is habitat dimension that determines the effective abundance of the scorpion. It is meaningless to talk about population density without considering habitat using in question.

C. RECKLESS BEHAVIOR

As pointed out in chapter 4, "reckless" describes the subordinate species' behavior of coming back to their preferred habitat at the peak density of the dominant species. This behavior, of course, is undefined for a dominant species such as *H. arizonensis*. Recklessness depends on three conditions. First, the species must show selectivity on its habitat use. Second, such fitness related selectivity must depend on the density of a competitively superior species. And third, both species must show some degree of preference to the same habitat type and compete for its use. Surprisingly, whenever these conditions met, the scorpions show such reckless behavior (table 36).

Reckless behavior is optimal. Assuming negative correlation of fitness and

Table 36. Summary of the experimental results, the scorpions' preferred habitats, and the reckless behavior.

HABITAT DIMENSION	<i>C. exilicauda</i>	<i>H. arizonensi</i>	<i>V. spinigerus</i>
vegetation cover			
preference:	open	open	open
depend on:	V.	H.	H.
reckless:	yes	no	yes
substrate			
preference:	fine	fine	no
depend on:	C.	no	no
reckless:	no	no	no
rock-size			
preference:	large	small	large
depend on:	C.	H.	no
reckless:	no	no	no
ground-level			
preference:	no	no	no
depend on:	no	no	H.
reckless:	no	no	yes

density, and assuming Ideal Free Distribution (Fretwell, 1972), let us picture the following scenario. Dominant species D lives sympatrically with the subordinate species S. Both species select habitat optimally. At low density, they all prefer habitat H rather than habitat L. As their densities increasing, the fitness for species S in habitat H declines faster than in habitat L. At a point the fitnesses in habitat H and L will match. And species S uses the two habitats indifferently. At the same point, species D still prefers habitat H, although it has already started to accept a small portion of habitat L. Habitat H provides species D higher fitness than habitat L does. Now, if species D's density increases further so that the two habitats provide them the same fitnesses, species D will treat the habitats indifferently. And the dominant species will distribute itself equally among the two habitats. Start from this point on, species D will devalue the fitnesses of species S equally in both habitats. Because habitat H initially has a higher fitness for species S than habitat L does, a constant deduction will not change the relative fitness value for species S in the habitats. So, if species S still optimize its habitat use, it should go back to its preferred habitat H (figure 40).

C. exilicauda showed reckless behavior in both the vegetation coverage and the substrate habitats (see figures 17 and 18). But the experimental test only confirmed the existence of such a behavior on the vegetation habitat. At low density the bark scorpions prefer the open habitat. They switch to the covered habitat when *V. spinigerus* become more abundant. So they depend on *V.*

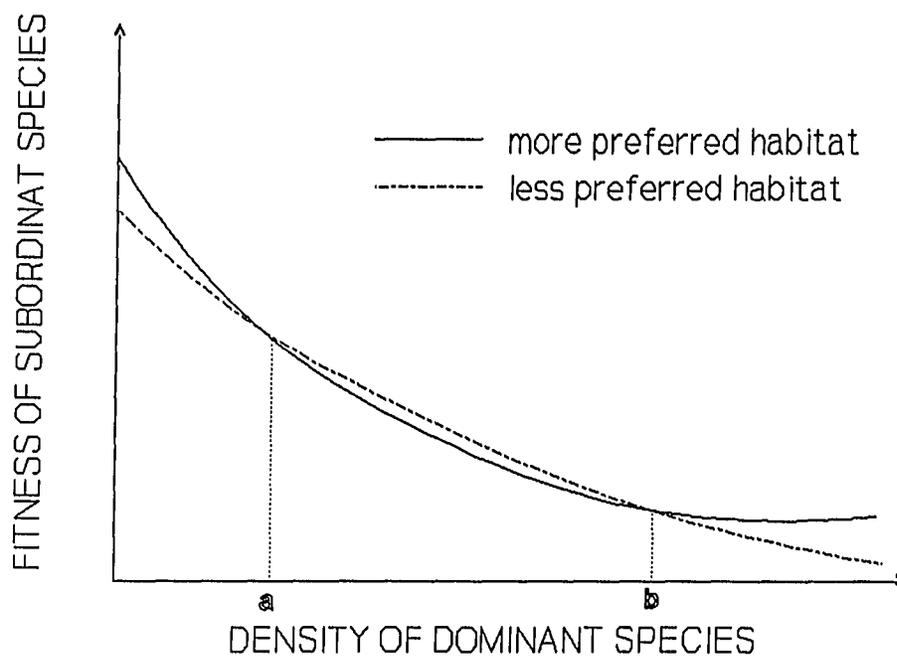


Figure 40. When the dominant species' density is $>a$, the subordinate species select its preferred habitat. When the dominant species' density is $>a$ and $<b$, the subordinate select the less preferred habitat. When the dominant species' density is $>b$, the subordinate select the more preferred habitat again. In the neighborhood of a and b , the subordinate has no preference on the two habitats.

spinigerus' density to make their choice on this habitat. But they switch back to the open habitat when *V. spinigerus* reaches its peak density. Notice here, the overall dominant species, *H. arizonensis*, did not influence the bark scorpions' behavior on habitat choice. On the other hand, *V. spinigerus* shown reckless behavior in both the vegetation coverage and the ground level habitats (see figures 32 and 38). And the experimental test confirmed them both. In both case, the striped tail scorpions' habitat choices depend on the density of *H. arizonensis*. Thus, the scorpions had formed a chain of density dependency. This chain obviously reflects the body-size order of the scorpions and their capability in competition.

In short, reckless behavior is a selective behavior. It optimize the fitness of the habitat selectors. By applying it, the subordinate scorpions did their best in a worst situation.

D. COEXISTENCE OF THE SCORPIONS

Heterogeneous habitats fostered the scorpions to coexist. No doubt about that. But, knowing the conditions for coexistence does not explain the mechanism that ensures the competitive scorpions to coexist. So a thorough understanding of the mechanism of coexistence demands more discussion. Again, body size difference and habitat differentiation of the scorpions require special attention

here.

In general, the scorpions used their habitats in three patterns. They are density independent, no preference, and density dependent. The last one comprises both inter- and intraspecific density-dependent. I will discuss each of these in turn.

The scorpions have distinguished their habitat preferences extensively. Some of the distinctions are so static that any density changes rarely influence the scorpions' selective behavior. The scorpions select these habitats density-independently. The continuous preferences of large rocks by *V. spinigerus* and of fine substrate by *H. arizonensis* fit this category. It makes good sense biologically. The striped tail scorpions are ground surface dwellers. They shelter underneath rocks and debris. Large rocks always provide the scorpions better protection either from harsh environmental conditions or from ferocious predators. So large rock habitat is one of the primary requirements for *V. spinigerus*. They just simply cannot afford to give it up. In contrast, the giant hairy scorpions are true burrowing creatures. So, fine substrate is one of their primary requirements for surviving. They cannot afford to lose fine substrate habitat either. The long evolutionary history made these species indispensable with these fundamental requirement. It certainly reflects the ghost of competition past. Yet, it is the differences in their primary habitat use that provide the basic platform for the

scorpions to coexist.

Not all the scorpions have preference on all the habitat dimensions studied. This also makes a good sense biologically. The bark scorpions are arboreal species. There is no reason for them to substantiate in the ground level habitats. Similarly, the striped tail scorpions are not true borrowing creatures. It is senseless for them to pry the substrate habitats and the ground level habitats. Notice that no preference on a habitat dimension does not necessarily mean the species' behavior in that dimension is not affected by the others. For instance, the striped tail scorpions shown no preference in the ground level habitats when they are rare. But they prefer the high-ground-level habitat when the giant hairy scorpions become intermediately abundant.

The most interesting arena along this line is the density-dependent habitat selection. As stated early, this category includes both intra- and interspecific density dependence. Intraspecific density-dependent habitat selection mainly occurred to the dominant species, *H. arizonensis*. And only once to the subordinate species *C. exilicauda* in the rock-size habitat. Probably, the bark scorpions used this habitat as a temporal shelter, which protected them from competitors and predators while hunting and traveling on the ground. The reason for *H. arizonensis* being exclusively intraspecific density dependent is easy to understand. Large body size guaranteed their competitive and predacious superiority to the other species of scorpions. And such powers put them in the

dominant position. The numerically dominant species, *V. spinigerus*, shown no sign of intraspecific density-dependent behavior. This is no surprising for a tolerant species.

Interspecific density-dependent habitat selection cast the major mechanism of coexistence. Because of its dynamic nature, interspecific density-dependent habitat selection itself promotes an array of interesting results. The reckless behavior discussed above is one of them. Another, and also related, is the behavior that occurred only to the bark scorpions. It appeared like this. *C. exilicauda* prefers the open habitat, and so do the other two species. *H. arizonensis* is the dominant species on this habitat. So logically *C. exilicauda* should use more of the covered habitats at high density of *H. arizonensis*. But what actually happened was the opposite. That is, *C. exilicauda* used more of the open habitats at high density of *H. arizonensis*. Before explaining the seemingly bizarre behavior, let us recall some useful facts. First, the average body size for *H. arizonensis*, *V. spinigerus*, and *C. exilicauda* are 9.99 cm, 6.88 cm and 5.58 cm respectively. Body size indicates the competitive strength of the scorpions. The more similar in body size the stronger scorpions compete. Thus, the strongest competition exists between *V. spinigerus* and *C. exilicauda*. Second, *V. spinigerus* are more mobile and five to eight times more abundant than *H. arizonensis* are. This increases the competition of *V. spinigerus* and *C. exilicauda* to a higher level. Third, *V. spinigerus* and *C. exilicauda* share more life history characteristics than

either one of them shared with *H. arizonensis*. And this magnifies the competition between them even further. Thus, *C. exilicauda* compete much more tempestuous with *V. spinigerus* than with *H. arizonensis*. This also explains why the bark scorpions depend mostly on the density of *V. spinigerus* to select their habitat. The best example that illustrate this point is the density dependent chain formed among the scorpions. On the vegetation habitat dimension, the bark scorpions depend mostly on the density of *V. spinigerus* to make their choice. The striped tail scorpions depend on the density of *H. arizonensis*. And the giant hairy scorpions depend on their own density.

Now it is the right time to integrate all the discussions together, and see how the scorpions' selective behavior on habitat use facilitates their coexistence. Because the ground-level habitats had a trivial effect to the scorpions, and because the substrate habitats were used density independently by *H. arizonensis* only and trivial to the others, I will discuss the scorpions from the intervening outcomes of both the vegetation and rock-size habitats.

Both *C. exilicauda* and *V. spinigerus* prefer the open and the large-rock habitats at the absent or low density of *H. arizonensis*. As *H. arizonensis*' density builds up, *C. exilicauda* and *V. spinigerus* switch to the less preferred covered habitat because *H. arizonensis* prefers the open habitat too. On the other hand, *C. exilicauda* and *V. spinigerus* did not change their rock-size preferences in accordance with *H. arizonensis*' density because *H. arizonensis* always prefers the

small-rock habitat. In the vegetation habitat dimension, *H. arizonensis* used up most of the open habitats. And *V. spinigerus* avoiding the competition and predation from *H. arizonensis* used up most of the covered habitats. Because the competition between *C. exilicauda* and *V. spinigerus* is severer than between *C. exilicauda* and *H. arizonensis*, and because *V. spinigerus* is denser than *H. arizonensis*, *C. exilicauda* switched back to the open habitat. The bark scorpions trade high predation risk with high completion pressure. On the other hand, *H. arizonensis* not only prey on *C. exilicauda* but also on *V. spinigerus*. And such predacious pressure maybe even higher to *V. spinigerus* than to *C. exilicauda* because they share the similar foraging tactics. The final solution is that *C. exilicauda* shares the open habitat with *H. arizonensis*, but differs rock-size habitat with *H. arizonensis*. So *H. arizonensis* acted inadvertently as the protector of *C. exilicauda* from *V. spinigerus*.

Thus, *C. exilicauda* is the subordinate species in this scorpion community. Its behavior of habitat use controlled directly by the density and behavior of *V. spinigerus*, and indirectly by the density and behavior of *H. arizonensis*. *V. spinigerus* is the tolerate species in the community. Its behavior of habitat use coarse by the density and consequently the behavior of *H. arizonensis*. However, because the intermediate body size, their behavior can unintentionally influence the behavior of *C. exilicauda*; and because their numerical dominance, their density can passively influence the behavior of *H. arizonensis* as well. Obviously,

H. arizonensis is the dominant species in the community. Its behaviors of habitat use depends exclusively on its own density.

In summery, different basic habitat requirements of the scorpions set up the primary requisition for their coexistence. Variations in competitive and predacious ability promote the scorpion to select different habitat, which consequently induced coexisting results. Thus, habitat selection played a substantial role in the organization of scorpion community.

E. COMPARISON WITH OTHER SCORPION COMMUNITIES

Studies conducted on scorpion community are rare. The majority of these studies discussed three major topics: species richness; numerical dominant or species distribution; and community structure.

Polis (1990) compiled data from 100 study sites worldwide and found that 8% of the sites had 1 species; 7% had 2 species; 21% had 3 species; 13% had 4 species; 12% had 5 species; 12% had 6; 10% had 7; 8% had 8; 6% had 9; and only 3% had more than 10 species. Most scorpion communities composed of three to seven species. With three species, the scorpion community in the West of Tucson Mountain fits this spectrum as an ordinary one.

The numerical distribution in three-species communities ranges from extremely skewed to evenly distributed. Lourenço (1975) worked with a three-

species community in Brazil and found the scorpions distributed lopsidedly (96.8%, 2.7%, and 0.5%). In contrast, Gertsch and Allred (1965) found a Nevada scorpion community distributed fairly even (40%, 35%, and 25%). The scorpion community in the West of Tucson Mountain fits between these extremes. 74.01% of the scorpions in the community was *V. spinigerus*; 14.39% was *C. exilicauda*; and 11.58% was *H. arizonensis*.

Both biotic and abiotic factors were hypothesized and studied to explain community structures in scorpions (Polis, 1990). The biotic ones included exploitation competition, interference competition, and predation. Heterogenous environment, random opportunity, and regular natural perturbation were considered the abiotic ones. Neither single factor could completely explain the community structure of scorpions. Williams (1970) found three species of scorpions coexisting in Phoenix South Mountain. He argued that the superior competitor *H. arizonensis* shared its habitat with two *Veajovis*, *V. spinigerus* and *V. confusus* because the scorpions utilized different size of prey. And the two *Veajovis* could employ different microhabitats. Working with the southern African *Opisthophthalmus*, Lamoral (1979) claimed that the scorpions' specific preferences on soil substrate reduced competition for burrow sites and promoted coexistence. Koch (1977, 1978, 1981) maintained that similar home site preferences and similar body sizes prohibited some Australian scorpions to coexist in the same habitat. The three species of scorpions in the West of the Tucson Mountains coexisted by

selecting various habitats. And such selection, imposed by competition and intra-guild predation, revealed dynamically the mechanism of coexistence.

F. CONCLUSION

Differentiation in habitat use is the main mechanism in constructing the scorpion community in West Tucson Mountain area.

Density-independently selected habitats provided the primary requirements for the scorpions to coexist. And density-dependently selected habitats promoted the scorpions to coexist optimally and in fine geographical scale. Heterogenous environment, depicted by mosaic habitat types, grants different habitat dimensions being available to the scorpion at the same time. Therefore, the scorpions can employ the density-independently selected habitats and the density-dependently selected habitats simultaneously. This enriched the scorpions' behavior in selecting habitats, and consequently enhanced their coexistence.

Body size of the scorpions reflects their competitive and predacious ability. Which, in turn, determines the main, if not all, structures of scorpion community in the West Tucson Mountain area.

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